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JAMES WATT MAVOR, PH. D.

PROFESSOR OF BIOLOGY IN UNION COLLEGE

General Biology

THIRD EDITION

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THIRD EDITION

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To

Dorothy Jessup Mavor

James Watt Mavor, Jr.

Huntington Mavor

205713

Preface

The purpose of this text is to state simply and clearly the main facts and principles on which a sound and teachable course in biology can be based. This requires that the balance between the botanical and zoological portions be such as to provide for a real grounding in each of these subjects. So far as is possible stress has been laid on facts which can be verified either in the laboratory or from common experience. Emphasis has been laid on the scientific method and the mode of presentation is designed to develop the habit of logical thinking in the student. The order in which the material is presented has been chosen both with regard to the logical development of the subject and to a close correlation between laboratory and classroom work. Nevertheless this order need not be strictly adhered to as the parts of the book are to a considerable extent independent. To give latitude to the teacher and make possible variations in the course from year to year in a number of cases alternative types have been discussed and sections have been written so that they may be omitted or included without serious loss of continuity.

The book is divided into six parts. The first part, on the nature of life, aims to develop a general foundation from which the scientific study of biology can proceed. The second part deals with plant life and takes up the various groups of plants, beginning with the simplest and ending with an account of the morphology and physiology of the higher plants. This plan is followed in the third part which deals with the lower animals (Invertebrates). The fourth part continues the account of animal life and is devoted to the anatomy and physiology of the frog and man. Rounding out the picture of the living processes the fifth part treats development and heredity in plants and animals. The sixth and last part aims to give a broad view of the organic world and its evolution.

The instructor may prefer to go rather rapidly through the first part and to follow this with the fourth part dealing with the anatomy and physiology of the frog and man, dissecting the frog in the laboratory at the same time. This may then be followed by the lower animals as treated in the third part or plants as treated in the second part. The text can be adapted to other sequences and adjusted to the time of the year and the part of the country in which the course is given. The material in the last two parts dealing with heredity and evolution would seem to come naturally at the end of the course.

The chapters in the separate parts of the book are also to a considerable extent independent although arranged in a logical sequence. Thus the first chapter in the first part on the method of science aims to orient the student, especially the beginner in science, toward the scientific approach. In the second chapter on the general characteristics of living things the scientific method is applied to the problem of what constitutes a living thing. The third chapter serves to broaden this first view and to give a brief survey of the world of organisms. In the fourth chapter attention is directed toward the cell as the fundamental unit of life in which the living processes are carried on. In the next three chapters which deal with the structure of matter, organic compounds and cell physiology the analysis is carried further into the inorganic.

Here again varied treatments are possible. The third chapter on the classification of plants and animals may be put over to the end of the first part or omitted entirely in favor of the discussions in the separate chapters of the second, third, and fourth parts. The fifth and sixth chapters on the structure of matter and organic compounds may be omitted or assigned as reading, especially in the case of students already familiar with chemistry and physics.

In the case of the second and third parts of the book which deal with plants and invertebrates it is assumed that the order of presentation will be that of the text although here again certain chapters and parts of chapters may be omitted. Thus in the second part Chapter 10 on the liverworts and mosses, Chapter 13 on the Gymnosperms, and Chapter 17 on the economic importance of plants may be omitted without interrupting the continuity. Chapter 12 on the alternation of generations may be read either after Chapter 10 on the liverworts and mosses or after Chapter 11 on the ferns and their relatives. Similarly parts of the third part may be omitted. This is especially true of Chapter 23 on the arthropods. Here the instructor may choose between the crayfish, grasshopper or bee as a type to be studied in detail.

Although revised throughout, the present edition differs from the two previous editions chiefly in Parts, I, V, and VI. In Part I a chapter on the characteristics of living things has been added, the chapter on the cell has been expanded and the chapter on the physical basis of life has been entirely rewritten and now forms three chapters dealing respectively with the structure of matter, organic compounds, and cell physiology. The chapter on the world of life in the earlier editions has now been moved to Part VI where it has been expanded to include a discussion of the environment and geographic distribution. The chapters in the second edition grouped under the heading "Principles" and placed in Part V are in this edition separated into two parts. One of these, Part V of this edition, contains the chapters dealing with development and heredity. The other part, now Part VI, entitled "The Organic World and Its Evolution" contains the chapters on evolution in Part V of the earlier editions and a chapter entitled "Animals and Plants in Relation to Their Environment." The chapter on the mechanism of evolution has been considerably expanded, chiefly by the addition of a section on "The Origin of Species in the Light of Present Knowledge." It is hoped that the small amount of elementary algebra necessarily introduced in the discussion of the application of statistical methods to the study of evolution will not preclude a consideration of this new and important field. In place of the detailed table of contents in the earlier editions, the table of contents in this edition has been reduced to a list of chapter headings and at the end of each chapter a topical outline is added giving in detail the contents of the chapter.

Acknowledgments

Since in a book of this scope space makes it quite impossible to cite authorities and original sources for all of the facts and theories discussed, and even if it were possible little would be accomplished beyond the distraction of the elementary student, all references to original sources, except in the case of illustrations, quotations, and a few special cases, have been omitted.

Acknowledgments for permission to reproduce illustrations are made in the legends with the illustrations. The author wishes, however, to express in this place his particular thanks to The Macmillan Company, Messrs. John Wiley and Sons, and the McGraw-Hill Book Company for permission to reproduce a considerable number of illustrations from their publications.

For original drawings and the redrawing of a number of figures from other texts, the author is indebted to Mr. August Swyka, Mr. James H. Purdy, III, and Mr. Edward W. Miller, former students at Union College, to Mr. J. C. Roberts of the New York State Conservation Commis-

sion, and to Miss Florence Dunn of Boston. For many of the photographs of plants and animals in their natural habitats the author is indebted to Mr. L. W. Brownell of Paterson, N. J. Mr. William Parker, formerly a student at Union College, was of great assistance in preparing the manuscript of the first edition for the press.

The author is under special obligation to the members of the Biology Department at Union College, both past and present, who cooperated in conducting the course at Union and read and criticized parts of the manuscript of the first edition. Dr. Ernest E. Dale read most of the manuscript, made many suggestions and gave much valuable criticism especially with reference to the botanical part. Dr. Leonard Clark read most of the manuscript and made many valuable suggestions regarding the zoological part. Dr. Allan B. Scott read the proof of Parts I and II. Dr. Ira B. Hansen, now of George Washington University, Washington, D. C., read and criticized the chapters on reproduction and development. Dr. Samuel Leonard, now of Cornell University, Ithaca, read and criticized the chapter on endocrines. Professor E. S. C. Smith of the Geology Department of Union College read and criticized the chapter on the history of life on the earth.

The author is particularly indebted to Dr. Ralph G. Clausen, formerly of the Union College Faculty, now of the New York State Teachers College at Albany, for assistance and contributions to the chapter on the world of life as it appeared in the second edition.

Two members of the Union College Faculty have contributed particularly to this edition. Dr. Manning Smith, recently of the Department of Chemistry, read and criticized the manuscript of the chapters on the structure of matter and organic compounds and was extremely helpful. Dr. Allan B. Scott read and criticized the chapter on the cell and made many useful suggestions. My wife has read and corrected the proof of many of the chapters and is to a considerable extent responsible for the index.

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PART I. The Nature of Life

"Of all human ambitions an open mind eagerly expectant of new discoveries and ready to remold convictions in the light of added knowledge and dispelled ignorances and misapprehensions, is the noblest, the rarest and the most difficult to achieve."

James Harvey Robinson

CHAPTER 1

The Scientific Method and Its Application to Biology

Science aims to give us an accurate and consistent mental picture of the world around us and of ourselves. To make this picture understandable, science tries to explain the varied phenomena which pass before our senses in terms of general laws. These general laws bring order into the picture. The knowledge which this mental picture has given to mankind has proved a very useful tool for solving practical problems and thus has had a tremendous effect on our way of life and standard of living. The success of science in providing this knowledge is due largely to the method which it employs. There is no more important intellectual possession or practical advantage to be gained from a study of science than a thorough appreciation of its method and scope.

1. A GENERAL OUTLINE OF THE SCIENTIFIC METHOD

The scientist is first and foremost an **observer** — an observer who tries to see things clearly and exactly as they are. But he does not stop here; he tries to explain what he observes. His explanation is usually given in the form of a general statement which correlates and brings into harmony a group or series of observations. Such a general statement, when first made and in its tentative form, is called an **hypothesis.** After an hypothesis has been formulated it must be tested, and it is here that the scientific method shows its particular merit.

Three types of **test** may be applied to an hypothesis. In the first of these, which is the more direct, **further observations,** similar to those which suggested the hypothesis, are made, perhaps under somewhat different conditions. Since the hypothesis is now definitely on trial, the observations may be of a more critical nature and designed to show specifically whether the hypothesis really covers the situation. These later observations may give further support to the hypothesis, or they may show that it needs modification, or that it should be abandoned entirely. In the second type of test, which is less direct, a **logical deduction** may be made from the hypothesis — a deduction which seems to follow necessarily from the hypothesis and to stand or fall with it. A new series of observations is now made to test for the occurrence of the phenomenon indicated in the deduction. If these new observations show that the indicated phenomenon occurs, the original hypothesis is supported; if not, the inconsistency must be explained. The third type of test requires the use of one or more **experiments.** In the experiment certain factors, usually variable in the natural occurrence of the phenomenon, may be controlled or kept constant, so that the particular relationship stated in the hypothesis may be more clearly demonstrated. An experiment is usually devised so as to determine whether a certain thing does or does not happen under a given set of conditions.

An example will make clear the differences between the three types of test. A careful dissection of the head of an insect reveals a slender strand of tissue extending from the "brain" to the eye. This leads to the hypothesis that this is the optic nerve along which nerve impulses pass from the eye to the brain. The first type of test applied to this hypothesis would involve the dissection of more specimens, and perhaps specimens of different species of insects, to determine whether the structure observed was of constant occurrence; also, a microscopic study of the tissue might be made to ascertain whether its structure resembled that of nerves in the other parts of the body. These observations would probably make it possible to determine quite definitely whether or not the strand of tissue really should be considered the optic nerve. In the second type of test the deduction might be made that if the tissue under investigation is actually the functional pathway for nervous impulses from the eye to the "brain," the strand of tissue ought to be thicker in insects with large eyes than in insects with small eyes and be absent in insects with no eyes. A series of insects with eyes of various sizes might be examined for this particular feature. If the structure and thickness of the strand of tissue was found to be correlated as above with the size of the eyes, the original hypothesis would receive considerable support. To apply the third type of test an experiment would have to be devised. This might consist, first, of a series of observations on the reactions of the insect to light, during which it might be observed that the insect moved away from a bright light. This determined, a delicate operation might be performed in which the strand of tissue extending from the "brain" to the eye was cut across. If, after the operation, the insect proved to be indifferent to the bright light, evidence of the conducting nature of the tissue would be obtained. But the experiment would have to be very carefully performed so as to make sure that only the particular strand of tissue under investigation was cut and also that the indifference of the insect after the operation was not due to some other effect or effects of the operation. This can be guarded against to a considerable extent by the use of control insects. In these insects all the details of the operative and experimental technique, with the exception of the actual cutting of the strand of tissue, would be carried out. If the experiment is to be used as evidence in support of the hypothesis, the control animals should behave toward the light in a normal manner or at least in a manner consistently different from the operated animals.

Sciences which, to a large extent, are limited to verifying hypotheses by the observation of phenomena as they happen to occur in nature, rather than in controlled experiments, are called **descriptive sciences.** Astronomy and geology are largely descriptive sciences. Sciences in which the experimental method is the one chiefly employed are called **experimental sciences.** Examples of such sciences are physics and chemistry. Some sciences, and biology is one of these, employ both methods and are therefore in part descriptive sciences and in part experimental sciences.

An hypothesis, to be accepted as a part of scientific knowledge, must not only offer a satisfactory explanation of the relevant observations but it must also be consistent with the principles which have already been laid down for the science. As generally used, there is not much difference between the terms hypothesis and theory, although there is a tendency to apply the term **theory** to an hypothesis which has been verified and related to other hypotheses in the field. Theories which have been long established and form the foundations of a science become laws or principles. The term **law** as used in science is generally applied to a somewhat restricted and precise generalization from a group of facts or observations. The term **principle** is usually applied to a wider and more inclusive concept or generalization. Thus the statement that "bodies attract each other inversely as the square of their distances and directly as their masses" is commonly referred to as the "law of gravitation," while the conception " that the present diversity of plant and animal life on this planet is due to a common descent from primitive ancestors with modifications in succeeding generations" is usually referred to as the principle of evolution. It should be emphasized that no law or principle of science can ever be regarded as absolutely proved; all are subject to modification with the accumulation of more data and the increase of knowledge. Science, like the material world of which it attempts to give us a picture, is itself in evolution.

A clear distinction should be made between the term "law of nature," as sometimes used in science, and the term "law of the land" or "civil law." A law of nature is simply a generalization based on all the known facts. A civil law is a regulation decreed by some social body and one which is to be obeyed by the individuals of a society. A law of nature cannot be broken. The occurrence of an exception to the law merely shows that the law is not so universal as was assumed. For example: That gunpowder explodes upon concussion is a natural law; that a person may not explode gunpowder on the street is a civil law.

As in the case of the word "law," the use of the word "principle" in science should be distinguished from its use with reference to human conduct where a "guiding principle" or an "ethical principle" is, like a civil law, a rule which should be followed rather than a generalization from observations.

A. OBSERVATION

An important factor in the precision of the scientific method consists in making a clear distinction between what is actually observed and the conclusions which may be drawn from the observations. The test of the **accuracy of an observation** is made when a number of independent observers agree regarding it, even when the conclusion or conclusions which they draw from the observation may be quite different. Some examples will make this clear. The ancient astronomers made many accurate observations of the movements of the stars and planets and the time of occurrence of celestial phenomena. In this way they accumulated data which are still used today in determining the time of eclipses and other astronomical events. Although the observations were made in the belief that the earth was the center of the universe and that all other celestial bodies revolved about it, this did not interfere with their accuracy. Or, to take an example from chemistry: The combining weights of many of the chemical elements were worked out with considerable accuracy by the early chemists. Not until long afterward were these data correctly interpreted and used to support the atomic theory of matter and the periodic table of the chemical elements. Coming to biology, in the first half of the sixteenth century, the great anatomist, Vesalius, made some of the most accurate dissections and drawings of the arteries and veins of the human body which have ever been made — known to be accurate because they have been repeated and verified by anatomists for four centuries. Yet he had no clear idea of the course of the circulation, which was not discovered until nearly a century later when these observations, along with others of an experimental nature, enabled Harvey to demonstrate the circulation of the blood.

All observations are not of equal value nor are all observers equally accurate. Observation, like all other activities, requires **training.** One of the most difficult parts of that training is to learn to be without prejudice, to observe without allowing any preconceived ideas to modify or influence the observation. It is, of course, impossible and undesirable for the observer to be without any knowledge of the significance and possible conclusions to be drawn from his observations, but it is an essential part of the scientific attitude of mind that the observer shall continually be on his guard against allowing these to influence his observations. They may show him what to look for but they must not affect what he sees. Let us take an example. Almost everyone has watched a robin walking over a lawn in search of worms. In doing this the bird usually turns its head to the right or left and takes a position strongly suggesting that it is listening for sounds from the ground. This assumption is, however, quite unwarranted. It is not difficult to demonstrate that the robin is looking for worms. Its eyes are on the sides of its head and it sees more clearly to the side than directly in front.

B. AN HYPOTHESIS

An hypothesis may be made early in the course of an investigation, indeed it may be made at the very beginning, as was probably the case in the earliest attempts to explain the presence of the sun, moon, planets, and stars; or it may not be formulated until after the accumulation of a large amount of data, as was the case in the development of the modern theories of the solar system and of the evolution of organisms. An hypothesis must be **precisely stated** and it must be **susceptible of verification** or disproof from data which have already been obtained or can be obtained. The situation may call for alternative hypotheses, one of which may be false while the other may be true. Although precisely stated and submitted to the most rigorous tests, an hypothesis is always regarded as a **provisional** working statement, subject to modification as the investigation proceeds and additional observations are made.

C. VERIFICATION OF AN HYPOTHESIS

An hypothesis is of no scientific value if it cannot be verified by observation. Thus the famous medieval thesis that an angel can stand on the point of a needle is entirely outside the realm of science, since by definition angels are not available for observation by mortals. Much of the beginner's practical work in science consists of the verification of already well-established hypotheses. This is not because new hypotheses and discoveries are not yet to be made in the fields studied, but rather because if the student is to benefit from what is already known in the science and to learn the methods which have been successful in the past, he can do this best in most cases by following the pathways which his predecessors have found with much effort and long labor. On the other hand, the student who regards practical work as merely seeing what he has been told to see will fail to get a clear understanding of the scientific method. Only by actually attempting to verify an hypothesis can a proper appreciation of the evidence for or against it, and the limitations to which it is subject, be obtained. Many significant discoveries in science have resulted from attempts to extend the appplication of hypotheses beyond the limits of the phenomena for which they were first intended. One of the most important characteristics of the scientific attitude of mind is an insistent demand on the part of the scientist for verification of his own hypotheses and the hypotheses of others.

D. THE EXPERIMENTAL METHOD

An experiment is usually devised to answer a question, and the success or failure of the experiment depends to a large extent on how clearly the question is stated and how carefully the experiment is planned to answer it. The question may be in the form of an hypothesis, the truth or falsehood of which is to be tested, or it may take the form of a request for quantitative or qualitative data. The fact that certain of the experimental conditions are determined by the experimenter, and in this way certain possibilities are ruled out, limits the number of possible answers to the question. The number of observations which must be made in order to reach a reliable conclusion is also reduced because, being made under similar conditions, they can be more accurately compared. The experimental method is well illustrated in a famous experiment on the generation of flies described in detail in a later section. The question asked was, "Do flies arise spontaneously or only from other flies?" Fresh meat was placed in each of two jars.[1] One of the jars was left open while the other was covered with gauze. Both of the jars were placed in a room where flies were abundant. In the meat in the uncovered jar abundant maggots, and eventually flies, developed. This jar and the meat it contained may be called the control. It serves to show that in the meat used and under the conditions of the experiment flies could develop. In the jar covered with gauze no maggots or flies developed. This shows, of course, that it was necessary for flies to get at the meat in order to have maggots develop in it. An experiment such as this ought to be repeated a number of times, but it is easily seen that a comparatively small number of observations in a carefully performed experiment would give a high degree of probability to the conclusion. The same result might have been obtained with the descriptive method by carefully observing how the maggots of flies develop, when it would have been found that they always come from eggs laid by flies; but to obtain an equal degree of certainty by this method would have probably required a large number of painstaking observations.

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[1] Actually a third jar was used, but it is not necessary to consider it in the present exposition. For a more detailed discussion of spontaneous generation and a description of this and other experiments see Chapter 2.

There is a tendency to regard the experimental method as more positive and certain in its results than the descriptive method. This, however, is not always the case. The law of gravitation, already referred to, is regarded as one of the fundamental laws of nature, yet it has only rarely and in special cases been submitted to direct experimental proof. Proof of the law for bodies on the earth's surface can be obtained by deduction from experiments on the rate at which bodies fall toward the earth. However, the general form of the law as applied to the planets and the other bodies of the solar system has depended for proof mainly on deduction and observation, since it is impossible to experiment with celestial bodies. Another example is that of the principle of organic evolution which is one of the fundamental principles of biology. This principle was developed as the result of many observations accumulated through the ages and especially in the last hundred years. It is clear that in so far as the principle states facts regarding the past history of life on earth, it is not susceptible of experimental proof, since it is not possible to experiment with the past. It may, however, be possible to obtain experimental proof that organic evolution is now in progress.

E. THE SYSTEMATIZATION OF SCIENTIFIC KNOWLEDGE

An essential part of the scientific method is the systematization, classification, and correlation of the information obtained. An observation or an hypothesis cannot be regarded as a contribution to science until it has been **correlated to existing knowledge.** The classification of scientific knowledge finds expression in the division of science into various branches and subbranches. But within each science there is a detailed classification of the findings of that science. Only by such an ordered arrangement can new facts or new hypotheses be related to knowledge already obtained.

2. THE SCOPE OF SCIENCE AND THE CLASSIFICATION OF THE SCIENCES

The nature of the scientific method excludes from the realm of science certain intellectual and emotional fields. Among the fields which are conspicuously excluded is that of the fine arts, especially music and painting. Although scientific discoveries have in some cases aided the technique of these arts, science has not contributed significantly to their main objectives. Nor has the scientific method yet been successfully applied to most of the problems in the field of the social studies.

The general field of science may be divided into special fields. However, no sharp lines can be drawn between the different sciences, and it is one of the great advantages of the scientific method that knowledge gained in one field can be directly transferred to another field. Thus facts learned in chemistry can be applied to the biological problems which arise in the study of respiration, digestion, or excretion; and facts learned in biology can be applied to the solution of chemical problems, where, for example, the discovery of oxygen came partly as the result of studies on respiration.

The word "science" comes from the Latin word, *scientia*, which means "knowledge," but the derived English word has come to be restricted to include only knowledge acquired by the scientific method. All of those sciences which deal with the phenomena of nature are grouped together as the natural sciences and contrasted with such abstract sciences as mathematics, which deals with the logic of measurement. The **natural sciences** may be divided into those which deal with nonliving phenomena, referred to as the inorganic sciences, and those which deal with living phenomena, referred to as the organic or biological sciences. The chief **inorganic sciences** are astronomy, geology, chemistry, and physics. Each of these has many subdivisions; and borderline sciences have developed in which one or more of them may be combined, as in physical chemistry.

The **biological sciences** include many different sciences dealing with particular fields. From the point of view of the kinds of organisms studied, the main division is into botany (Gr. *botane*, an herb), which deals with plants, and zoology (Gr. *zoon*, an animal + *logos*, a discourse), which deals with animals. The science of **botany** may itself be divided into

cryptogamic botany (Gr. *kruotos*, hidden + *gamos*, marriage), which deals with the nonflowering plants, and **phanerogamic botany** (Gr. *phainein*, to show + *gamos*, marriage), which is the science of the flowering plants. **Bacteriology** (Gr. *bacterion*, a little rod), which deals with bacteria, is really a branch of cryptogamic botany. Similarly **zoology** is divided into subsciences depending on the groups of animals studied. Thus there is **protozoology** (Gr. *protos*, first), which is concerned with the unicellular animals; **entomology** (Gr. *entomon*, an insect), the study of insects; **ichthyology** (Gr. *ichthus*, a fish), which treats of fishes; **ornithology** (Gr. *ornis*, *ornithos*, a bird), the study of birds; **mammalogy** (L. *mamma*, a breast), the study of mammals; and **anthropology** (Gr. *anthropos*, man), which deals with man.

From a different point of view, biology may be divided into another series of subsciences. Thus **morphology** is the study of the form and structure of organisms; **physiology** is the study of the function of organs and parts of organisms; **taxonomy** is the study of the classification of plants and animals; and **paleontology** is the study of fossils. The study of **organic evolution,** which deals with the succession of plant and animal types and how one descended from another, is also a branch of biology. **Genetics,** or the study of heredity, is another branch. **Ecology** is the study of organisms in relation to their inanimate surroundings and to the other organisms which influence their lives. Again, any one of these sciences may be divided into subsciences. Thus the science of morphology is divided into **anatomy,** which is the study of the gross structure of organisms; **histology**, which is the study of tissues; and **cytology,** which is the study of cells. There is also a science of comparative morphology — with branches of comparative anatomy, comparative histology, and comparative cytology — which is concerned with the comparison of the structures of different plants and animals. The principles and results of physics and chemistry are frequently applied in biology, and this has led to the development of the sciences of **biophysics** and **biochemistry.**

3. SOME FEATURES OF THE SCIENTIFIC METHOD

A. THE OBJECTIVE ATTITUDE IN SCIENCE

Science is objective, that is, it tries to represent the material world in a detached and impartial way, free from prejudice, emotion, or authority, other than that which must attach to skill in the use of its method. Science does not deny the value of emotion in stimulating thought and action, but it simply does not and cannot employ it in its method of searching for truth. Nor does science deny the concept of purpose in the universe. Here again it simply does not admit the postulation of a particular purpose as an explanation of a natural phenomenon. Its aim is to record the facts as they are presented to the senses, and by means of generalizations and deductions to weld them into a rational system. How this system can or should fit into the whole field or knowledge and man's relation to knowledge has generally been regarded as outside the field of science.

B. THE ANALYTICAL POINT OF VIEW

An important feature of the scientific method not yet emphasized is its employment of analysis. In attacking a scientific problem it is quite usual to try to break it up into simpler problems which have the prospect of simpler or easier solutions, or some of which may have already been solved. Thus the general problem of how a plant gets its food materials becomes divided into a number of subordinate problems, such as what raw materials are used, where the energy comes from, what the first steps are in the chemical changes involved, etc. By thus dividing the main problem attention can be focused on the subordinate problems, either one at a time or in groups. Analysis thus leads to a clearer and more concrete statement of the problem.

C. PREDICTION AND DISCOVERY IN SCIENCE

Probably no feature of the scientific method appeals more strongly to the popular mind than the way in which it has made possible the accurate prediction of the course of natural phenomena and the discovery of new materials and processes. A **famous case** was the prediction and subsequent discovery of the planet, Neptune. By using the law of gravitation, the exact shape and size of the orbits of the planets in their movement about the sun can be calculated. However, certain irregularities in the orbit of one of the planets, Uranus, could not be accounted for by the attraction of the other planets. To explain these irregularities a new planet was assumed, and the position which it would have to occupy in order to cause the irregularities was calculated. A new planet, Neptune, was discovered almost immediately in the exact position predicted. Another striking case was that of the prediction of the existence and characteristics of the chemical element, Germanium, by the Russian chemist Mendelejeff in 1871, and its subsequent discovery by the German chemist, Winkler, in 1886. Predictions have also been made in biology, but because of the large number of variable factors in living processes and the development and evolution of animals and plants, they have usually not been of so definite a nature as in the physical sciences.

D. THE MECHANISTIC AND VITALISTIC CONCEPTIONS

Two opposing views or conceptions are held regarding the ultimate explanation of biological phenomena. One, the vitalistic conception, to which the term vitalism has been applied, conceives that in living processes there is present a vital force or directing principle which is fundamentally different from the forces which act to bring about changes in inorganic matter. This vital force has been defined in various ways and to it different terms have been applied. The other, the mechanistic conception, finds or expects to find a complete explanation of living processes in terms of the conceptions of physics and chemistry. This does not mean that organisms are machines in the restricted sense in which that term is commonly used. They do not consist of pistons, cylinders, and wheels. Rather does it mean that an organism is an arrangement of parts which interact to produce certain end results, and that the interactions all proceed according to physical rather than extra-physical laws.

During the earlier stages in the development of the science the vitalistic conception dominated biological thought, as will be made evident in the following section discussing the history of biological problems. However, as the science has developed, one after another of the vital processes has been found to be capable of an explanation on the basis of the known laws of physics and chemistry, and the vitalistic conception has been pushed more and more into the background. It must be admitted, nevertheless, that there are many phases of living things that cannot at present be explained on a mechanistic basis.

4. EXAMPLES OF THE APPLICATION OF THE SCIENTIFIC METHOD TO BIOLOGICAL PROBLEMS

It is difficult for the student or investigator today, provided with the modern microscope and descriptive textbooks, to realize the long and tortuous path along which his predecessors had to travel. Facts and observations which eluded or baffled the greatest minds of the past now seem simple and clear. The very ease and rapidity with which we can now pass in review scientific principles which took centuries to establish makes us to some extent lose sight of their value and significance and of their proper place in the realm of human thought and endeavor. New discoveries in biology, as in the other sciences, come rapidly and, thanks to our accumulated knowledge and technique, relatively easily today. But the fundamental discoveries on which these are based came slowly and were accepted only after much misunderstanding and controversy.

The history of science may be arbitrarily divided into epochs. Science may then be considered first in antiquity, in Egypt, Ancient Greece, and Rome, second in the Dark Ages extending from the second to the eleventh century A.D., third in the Renaissance extending to the sixteenth century, and fourth in modern times. We may best appreciate the state of science in these epochs by following the solutions of some of the fundamental problems of biology as they were gradually worked out through the ages by great thinkers and scholars.

A. THE FOUNDING OF MORPHOLOGY

From the earliest times man has been interested in the structure of his own body and of those of the higher animals which he has hunted or domesticated. Among the many drawings and sculptures left by the men of the Early Stone Age (about 25,000 B.C.) many show with considerable accuracy the muscles of the legs and heads of such animals as the horse, bison, and mammoth. One shows the location of the heart in an elephant. The records of the ancient Egyptians, Babylonians, and Assyrians show that they had considerable practical knowledge of anatomy and performed somewhat complicated surgical operations. In the library of the New York Historical Society is an early Egyptian papyrus, dated about 2700 B.C. and attributed to Imhoteb, the great surgeon and architect of the Pharaohs. The heart is there described as a central organ from which vessels are distributed to the different parts of the body. In the Palace of Ashurbanipal, who ruled Assyria from 668 to 626 B.C., is a bas-relief of a dying lioness in which the superficial muscles are represented with striking realism. An arrow has pierced the spinal cord and paralyzed the hind limbs.

It is doubtful, however, if a science of anatomy existed before the Greeks and we turn to **Aristotle** (384–322 B.C.), who was the son of a physician, for the beginnings of the science of anatomy, or rather comparative anatomy, for it seems almost certain that he never dissected the human body. In his *Historia animalium* and *Partibus animalia* good descriptions of many of the organs of the higher animals, sometimes accompanied by drawings, are given and some of the terms which he used are still retained in a modified form today. Although remarkable for accuracy and the insight of the author, Aristotle's work contains many notable errors. For example, he attached little importance to the brain, making the heart the seat of intelligence, an idea which persists to this day in our metaphorical use of the word. Some years after Aristotle's time (about 300 B.C.) there lived in Alexandria, the great center of Greek learning in Egypt, Herophilus of Chalcedon, who has been called "the father of anatomy." He is said to have been the first to dissect both human and animal bodies in public, i.e., before an audience. Among his works was a book on anatomy, which has come down to us only through the works of others. He studied the brain, recognizing it as the seat of nervous activity, and distinguishing nerves into sensory and motor.

Not until nearly five hundred years later do we find a really great figure in anatomy. He also was a Greek. **Galen** (A.D. 131–200) was born in Asia Minor and went to Alexandria for his medical education, but did most of his work in Rome under the great emperor Marcus Aurelius. Galen was an original investigator and "one of the great anatomists and physiologists of all times." "In cases of controversy as to structure or function, his method was always to appeal to dissection and experiments." During the interval between Herophilus (about 300 B.C.) and Galen (second century A.D.) dissection of the human body was prohibited by law as it is today in certain parts of the world. Galen dissected the human body, but much of his work was done on animals such as the Barbary ape and the ox. He dissected and described in detail the brain, spinal cord, and nerves of the ox, showing how the nerves arise from the brain and the spinal cord and connect with the muscles. The best known of Galen's many books which were written in Greek is his *Administrationes anatomica*, or *Anatomical Procedure*, really a book on dissection, which originally contained sixteen volumes, only nine of which have survived in Greek, the remaining seven coming to us through an Arabic version. The works of Galen remained the authority in anatomy and physiology for more than a thousand years, until the Renaissance.

The spirit of the Dark Ages from the third to the eleventh century A.D. was hostile to science, much of the knowledge left by the ancients was lost, and what remained was accepted blindly without any real appeal to nature. Then in the Middle Ages came the founding of universities. In the beginning "the chair" of a professor was very much of a physical reality, a great elevated structure provided with steps and a reading desk, something like a pulpit. From there he lectured while a junior colleague pointed out the line of incision and a demonstrator performed the actual dissection. All was thus done third hand and according to the written word. The students in cap and gown stood in attendance but did no dissection (Fig. 1:1).

The real founder of modern anatomy was **Andreas Vesalius** (1514–1564), who was born in Brussels. "As a boy he was constantly dissecting the bodies of animals. Such tastes are common enough with boys nowadays. Nature study is taught in our schools, and it is easy to get help and hints from books. In the days of Vesalius the study of nature was little regarded, and no such books had been written. Vesalius had to find his own way."[1] "At the age of sixteen he went to Paris to study medicine."[2] "His impetuous nature was shown in the amphitheatre where at the third lecture, he pushed aside the clumsy surgeon barbers and himself exposed the parts in the proper manner. He could not be satisfied with the printed page; he must see with his own eyes, grasp through his own senses the facts of anatomical structure." [3] Vesalius went later to Padua in Italy where immediately after receiving his degree of Doctor of Medicine he was placed in charge of the teaching of Anatomy in the University. When only twenty-nine years of age he published in the year 1543 his great book on the structure of the human body entitled *De humani*

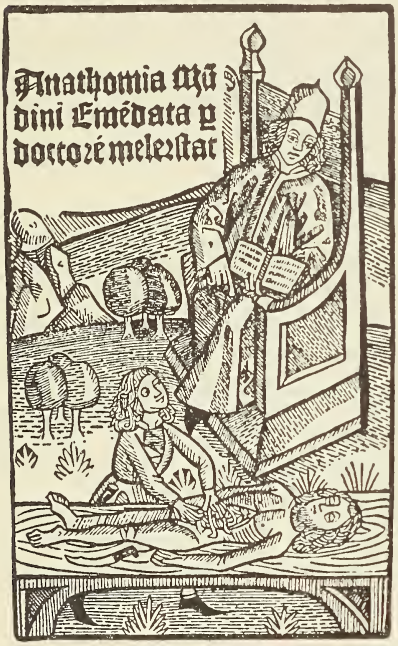

Fig. 1:1 The teaching of anatomy in the Middle Ages. The only illustration in a treatise on anatomy by Mundinus, also called Mondino, published in Leipzig in 1493. The demonstrator in the foreground is probably Alessandra Giliani, a young woman of unusual skill in dissection and a passion for anatomy, who was one of Mondino's assistants. From W. A. Locy, *The Growth of Biology*, by permission of the publishers, Henry Holt and Company, Inc.

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[1] Singer, Charles, *Evolution of Anatomy*, London, 1925.
[2] Locy, W. A., *The Story of Biology*, New York, Garden City Publishing Company, 1934.
[3] Singer, Charles, *ibid.*

corporis fabrica (*On the Structure of the Human Body*), illustrated by beautifully engraved plates.

With the work of Vesalius the general facts regarding the gross structure of the human body may be considered established. The founding of the science of comparative anatomy came later and was not achieved until the latter half of the eighteenth century and the beginning of the nineteenth. Most prominent among the biologists of this latter period was the Frenchman, **Georges Cuvier** (1769–1832). He dissected and compared many animals. *Leçons d'anatomie comparée* and *Le Règne animal distribué d'après son organisation* are his best known works. Cuvier also studied fossils and is regarded as the founder of the science of the paleontology of the back-boned animals (vertebrates). He was a man of wide knowledge and great attainments. Under Napoleon Bonaparte he became director of higher education for the Empire.

The investigation of the detailed structure of animals and plants, especially the smaller forms, had to await the application and perfection of the microscope in later centuries and will be referred to in another section.

B. THE FOUNDING OF PHYSIOLOGY

Knowledge of the structure of the body preceded a clear understanding of the functions of its organs. The Alexandrian school to which Herophilus, already referred to, belonged, expounded the idea of a **pneuma** or spirit of life. The pneuma was believed to enter the body by way of the windpipe and to pass in the arteries, which according to this theory were devoid of blood, to the various parts of the body. The veins alone carried the blood which nourished the body. The expression "animal spirits" which we use today, in a somewhat different sense, is no doubt a survival of this ancient idea. Galen corrected this conception to the extent of maintaining that the arteries carried blood to the organs, but he regarded the liver as the center of the venous system and believed that there was an ebb and flow of the blood to and from the heart in both the arteries and veins.

The work of Vesalius paved the way for a more rational physiology. The discovery of the **circulation of the blood** cannot be regarded as the work of one man. **Leonardo da Vinci,** that universal genius more generally known as an architect and painter than as a scientist, came very near to it. **Michael Servetus** (1511?–1553) described the lesser circulation, i.e., the course of the blood from the right side of the heart to the lungs and back to the left side of the heart in 1553. The book and its author were burned at the stake by order of the church. That the blood in the veins flowed toward the heart was discovered by **Andreas Cesalpinus** (1519–1603), better known for his botanical researches. The valves in the veins which permit the blood to go only toward the heart were discovered and figured by **Fabricius** (1537–1619).

The man who provided the clearest proof, and to whom credit is usually given for the discovery of the circulation of the blood, was **William Harvey** (1578–1657). Harvey begins his book, *Exercitatio anatomica de motu cordis et sanguinis in animalibus* (*On the Motion of the Heart and Blood in Animals*), published in 1628, with the words, "In discussing the movements and functions of the heart and arteries, we should first consider what others have said on these matters, and what the common and traditional viewpoint is. Then by anatomical study, repeated experiments, and careful observation, we may confirm what is correctly stated, but what is false make right." [1] To the previous knowledge, derived chiefly from the dissection of dead bodies, Harvey added many observations on the living animal. With the aid of experiments, and reasoning from the structure of the heart, he demonstrated that there is a circulation of the blood and that this is of a double nature: one course, known as the lesser or pulmonary circulation, taking the blood from the heart to the lungs and back to the heart and the other course known as the greater or systemic circulation, taking the blood from the heart to the rest of the body including the muscles, brain, digestive and other organs of which it is composed and back to the heart again. He showed also that the blood leaves the heart in the arteries and returns to it in veins. But he did not show exactly how the blood gets from the arteries to the veins.

The small tubes or capillaries in which the blood passes from the arteries to the veins were discovered some years later (1660) by the Italian anatomist and histologist, **Marcello Malpighi** (1628–1694), who also observed the movement of the blood through them. The great Dutch microscopist, **Antony van Leeuwenhoek** (1632–1723), who worked with a simple magnifying glass, gave a clear visual demonstration of the circulation in 1688 (Fig. 1:2). Describing his observations on the transparent tail of a tadpole, he wrote: "A sight presented itself more delightful than any mine eyes had ever beheld; for here I discovered more than fifty circulations of the blood in different places, while the animal lay quiet in the water, and I could bring it before my microscope to my wish. For I saw not only that in many places the blood was conveyed through exceedingly minute vessels, from the middle of the tail to the edges, but that each of the vessels had a curve or turning, and carried the blood back toward the middle of the tail, in order to be again conveyed to the heart. Hereby it plainly appeared to me that the blood-vessels which I now saw in the animal, and which bear the name of arteries and veins are, in fact, one and the same; that is to say, that they are properly called arteries so long as they convey the blood to the furtherest extremities of its vessels, and veins when they bring it back to the heart." [1]

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[1] *Exercitatio anatomica de motu cordis et sanguinis in animalibus*, by William Harvey, M.D., translated by Chauncey D. Leake, Tercentennial Edition, 1928, Introduction, p. 7.

Today no one speaks of the circulation of the blood as a theory. It has become a demonstrable fact, a fundamental conception in science. The proof of the circulation of the blood had a great effect on the development of the science of physiology. It offered a striking case of the mechanical explanation of a vital phenomenon.

It would take us too far to trace the development of physiology since the time of Harvey. Much of the advance has been due to the application of the discoveries of physics and chemistry to the investigation and the explanation of physiological phenomena. In this work many investigators in England, France, Germany, Holland, Spain, Italy, Russia, and America have taken part.

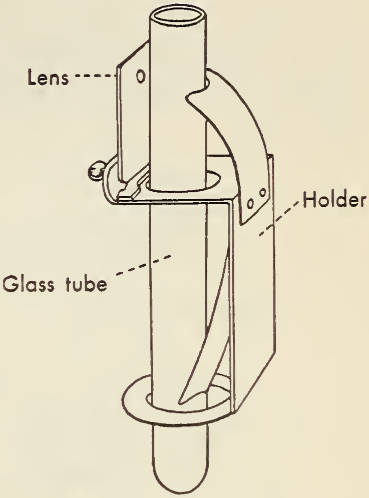

Fig. 1:2 The instrument with which Leeuwenhoek discovered the circulation of the blood in the tadpole's tail. The simple lens is in the brass plate on the left. The tadpole was placed head down in the test tube. Redrawn after an illustration in A. van Leeuwenhoek's selected works in English, 1758, reproduced in W. A. Locy, *The Growth of Biology*, by permission of the publishers, Henry Holt and Company, Inc.

C. *THE WORK OF THE EARLY MICROSCOPISTS*

Although the use of lenses to enlarge objects seems to have been known to the ancients and the compound microscope was invented in the sixteenth century, microscopes simple or compound do not seem to have been extensively applied to the study of animals and plants until the middle of the seventeenth century.

A **simple lens** or "magnifying glass" consists of a single piece of glass, ground and polished so as to have one or both surfaces convex, or of two or more pieces of glass placed together. The size an object appears to have depends on its distance from the eye (really on the angle which its outline subtends at the eye). Thus near objects are seen as larger and in more detail. The normal human eye cannot, however, see an object distinctly if it is nearer to it than 10 inches. The purpose of the magnifying glass (and also, in effect, of the compound microscope to be referred to later) is to produce the effect of having the object close to the eye, and therefore subtending a greater angle, while still appearing distinct (Fig. 1:3).

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[1] From Locy, W. A., *Biology and Its Makers*, New York, Henry Holt and Company, Inc., 1908.

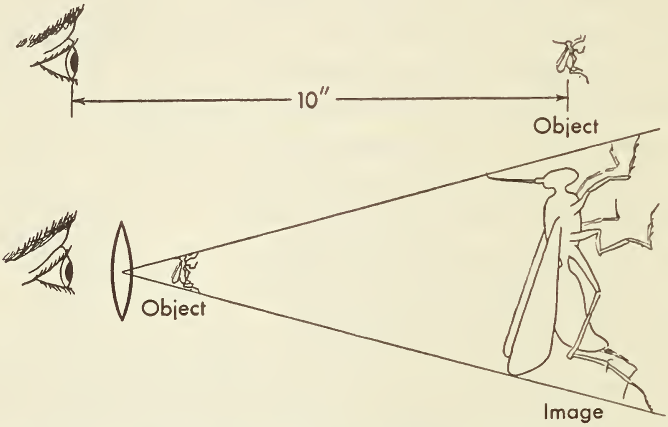

Fig. 1:3 The use of a simple convex lens to magnify an object. The effect is to make the object appear as if closer to the eye and therefore larger.

The greater the convexity of the lens the greater the magnification and the shorter the focus. Because of their short focus, lenses giving a high magnification are always small in diameter and must be held close to the eye and close to the object to be magnified. The magnified image is always fainter than the original object because when an object is magnified the light coming from it is spread over a larger area of the retina (the sensory layer in the eye) than would be the case were it not magnified. The use of a lens of high magnifying power, therefore, necessitates strong illumination of the object.

There is some doubt regarding the inventor of the **compound microscope.** Such microscopes were in use during the early part of the sixteenth century. The compound microscope may be thought of as consisting of two simple lenses arranged one in front of the other so that the second magnifies the image produced by the first (Fig. 1:4). The lens nearest the object is known as the objective and the lens near to which the eye is placed is known as the eye-piece or ocular. In modern compound microscopes the objective usually consists of two or three lenses set into a small tapering brass tube. Single lenses of high magnification have two defects from the point of view of the microscopist. They tend to break up white light into the component parts of the spectrum and hence to produce images which show a confusion of colors (chromatic aberration) and if ground so that their surfaces are parts of spheres to distort objects near the edge of the field of vision (spherical aberration). These two defects are corrected by using a combination of lenses of different kinds of glass for the objectives and another combination of lenses for the ocular. Many accessories which are mainly concerned with holding the object, adjusting its distance from the objective (focusing) and passing light onto or through the object (illumination), are added to the microscope of today.

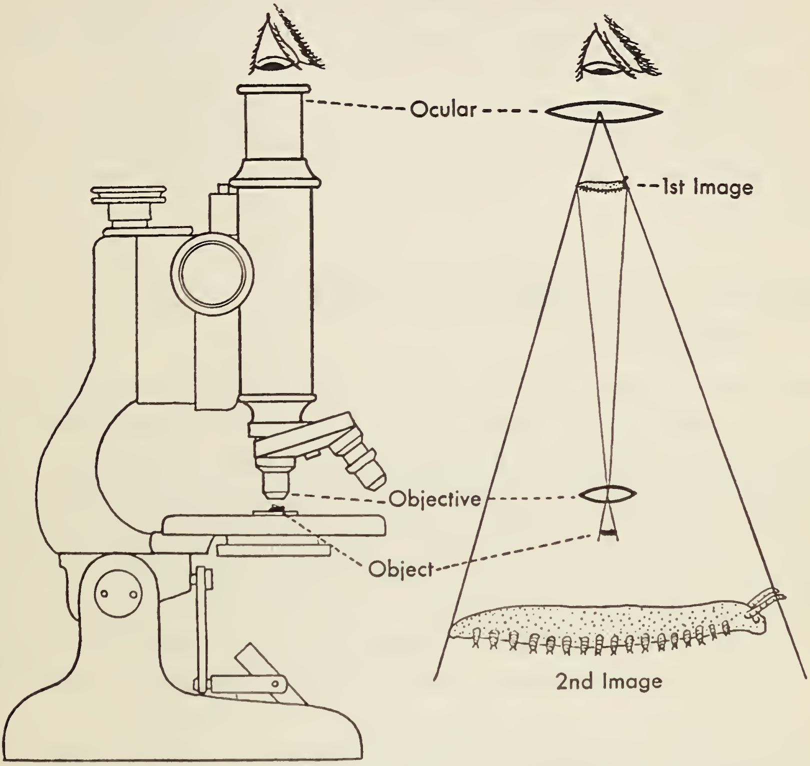

Fig. 1:4 The use of the compound microscope. At left, the microscope; at right, the lens system. The first image close to the eye is magnified a second time, making it still larger.

Among those who early applied the microscope to biological investigations, the names of three men stand out, **Marcello Malpighi, Jan Swammerdam** (1637–1680), a Dutchman, and **Antony van Leeuwenhoek.** Two of these have already been referred to as discoverers of the blood capillaries. Certain bodies in the kidney are named Malpighian corpuscles in honor of Malpighi. He is usually regarded as the founder of the science of histology. He dissected and examined both plants and animals and made extensive observations and drawings of the development of the chick within the egg. Swammerdam collected and dissected insects and made beautiful drawings of the details of their anatomy. Reference has already been made to Leeuwenhoek's observations on the circulation of the blood in the tadpole's tail. He was the first to describe the spermatozoa or male germ cells, the protozoa, and bacteria. These men were followed during the eighteenth century by a number of brilliant and accurate investigators with the microscope who paid particular attention to the minute anatomy of insects.

It is to be noted that all three of these men, Malpighi, Swammerdam, and Leeuwenhoek, probably did their best work with simple magnifying glasses. We know this to have been the case with Swammerdam and Leeuwenhoek.

5. BIOLOGY IN THE SERVICE OF MAN

A. *AGRICULTURE*

Most farmers would hesitate to call themselves applied biologists, yet it does not require much insight to see that in their work they are concerned with the application of biological facts and principles to the raising of crops and animals. Anyone who has come in contact with farming knows that there is a great deal more involved than the mere sowing of seeds and the reaping of harvests. The crop must be suited to the climate and soil, and the soil prepared for the crop. The feed must be the right kind, quality, and quantity. In ancient times and even until comparatively recently, tradition largely governed the practices of the tiller of the soil.

An important branch of the federal government of the United States is the **Department of Agriculture.** One of the chief duties of this department is to maintain agricultural experiment stations. In addition each state of the Union has one or more agricultural experiment stations. In the laboratories of these experiment stations researches are carried out on soils and their suitability for different crops, resistant and productive varieties of plants are bred, and methods of combating diseases developed. Nearly every state has one or more agricultural colleges where specialists in the various branches are trained. One of the chief duties of these institutions is to give free advice to farmers on their problems.

Famine stalked before ancient man and still appears in certain less enlightened parts of the world. Thanks to scientific methods of farming, the control of plant diseases and injurious insects, and the organization and distribution of production, the fear of famine is no longer a factor in the Western Hemisphere in time of peace.

B. CONSERVATION

In early times when men were few and the world seemed large, there was little need for the conservation of natural resources. Now as all parts of the habitable regions are rapidly becoming occupied by man and his works, preservation of forests and useful animals is becoming a problem of greater and greater importance. Conservation is necessary not only that the natural resources may be available, but because their depletion has far-reaching effects on climate and society. We are already beginning in the United States to feel the effects of the destruction of our forests and the squandering of lumber in the droughts that visit the central states, for much of the moisture that goes into the air is evaporated from the leaves of trees. Effective conservation of natural resources can be carried out only after detailed biological surveys and extensive studies of the principles involved have been made by expert biologists.

C. *FISHERIES*

The landsman is apt to think of **fishing** as chiefly a vacation sport. However, for many people it provides a livelihood and for a still greater number an important food. Most of our food fishes come from the sea; many of them from the deep sea. Only a few such as the white fish of the Great Lakes come from fresh water. Two methods are commonly used in commercial fishing: traps and nets.

Fish traps are usually set in shallow water and consist of a lead which the fish tend to follow into a pound where they are caught. From the pound the fish are gathered into small boats. Nets are of different types but the two principal kinds are the seine and trawl. Seines are used in shallow water where they may be hauled in by hand or with teams of horses, or they may be set in the open sea and hauled in by hand into small boats. The fishermen usually endeavor to set the seine around a school of fish or where they know fish to be abundant. A trawl net is a huge bag which is towed behind a boat. For deep sea fishing steamboats known as trawlers are used.

The **shellfish industry** is almost as important as the fishing industry proper. Shellfish are caught commercially by hand and by dredges from small boats and even steam tugs. On certain parts of the Atlantic coast the shallow water off shore is "farmed out" in oysters, the fishermen farmers having definite areas which they "seed" with oyster fry.

The fishing industry is one of which the public does not see much except the product at the dinner table, but it is one which employs a large number of people and receives considerable attention from the government in the form of regulation and research. That the development and control of fisheries is a biological problem goes without saying.

D. MEDICINE

It is scarcely necessary to stress the interdependence of biology and medicine. The physician of today is largely concerned with the application to particular cases of discoveries made in the research laboratories of medical schools and other special research institutions — in laboratories of physiology, of biochemistry, of bacteriology, and of experimental surgery. The researches are in most cases carried out on animals. A knowledge of the animals is of course necessary for the interpretation of the results. The death rate from all causes in the United States was, in the year 1880, approximately 20 persons per year per 1000 of the population, or 2 per cent. Forty-four years later in 1924, it was approximately 12 persons per 1000, a decrease of over 40 per cent. During the same period similarly striking decreases have been recorded for the various European countries. While the advance of medical science cannot be regarded as the only reason for this, it undoubtedly has been one of the primary and most important factors.

E. PUBLIC HEALTH

We may liken the life of a man to a game of skill in which his opponent is the ever-present and relentless environment, both living and dead, and the rules are the inviolable laws of nature. He who plays the game skillfully according to the rules lives happily and long while he who blunders or disobeys the rules is unhappy and short-lived. Most large cities have **departments of public health,** the chief duty of which is to guard the public against epidemics of infectious diseases. Through the activity of their public health laboratories, their field workers, and the cooperation of physicians, the following infectious diseases may be considered to be under control: diphtheria, tetanus, hydrophobia, typhoid fever, scarlet fever, smallpox, plague, cholera, and measles. It is appalling to think what would happen were one of our large cities, even for a short time, without the protection of its public health department. During the years of the Great Plague or Pestilence in Europe in the fourteenth century, it is estimated that in some parts of Europe two-thirds or three-quarters of the population died from the disease, and that the proportion was even higher in England. Today the plague is practically unknown in Europe and America.

F. SOCIETY

It is gradually being recognized by social philosophers that the living of men together in groups is a biological phenomenon, comparable in some ways with the social groups formed by animals, and that perhaps something may be learned about human society by studying animals.

War is a scourge of humanity not without its biological causes and effects. There can be little doubt that in the past wars have selected for their victims the physically and mentally fit. It is possible that a better knowledge of the biological causes and effects of wars would serve in a measure to prevent such conflicts.

The application to man of knowledge gained from the breeding of plants and animals is finding its expression in the eugenic movement for the betterment of the race. This movement depends largely on the enlightenment of the public regarding the inheritance of human characteristics and the care of the mother and child.

According to the Apocalypse, four horsemen ride over and terrify humanity. The first of these is named Pestilence, the second, War, the third, Famine, and the fourth, Death. Against each of these four horsemen, man has at least one effective weapon — biology.

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Questions

1. How does the method of science differ from other methods of obtaining knowledge? Illustrate your answer by discussing how a problem would be attacked by the different methods.
2. When is an observation to be accepted as accurate?
3. Distinguish between an hypothesis and a speculation.
4. Which of the following problems would be in the field of the physical sciences and which in the field of the biological sciences: (*a*) the age of the earth; (*b*) the origin of man; (*c*) the composition of the atmosphere; (*d*) the cause of typhoid fever; (*e*) the movement of the tides; (*f*) the food value of sugar?
5. To which branch of biology would the investigation of the following belong: (*a*) the arrangement of the bones in the hand; (*b*) the contraction of muscle; (*c*) the different kinds of roses; (*d*) the different kinds of butterflies; (*e*) the breathing of insects; (*f*) the formation of starch in a potato?
6. Which of the following would you consider as involving applied science: (*a*) playing a musical instrument; (*b*) the manufacture of an automobile; (*c*) the painting of a landscape; (*d*) the growing of wheat?
7. Outline the founding of the science of anatomy. What were the chief contributions of the following: Vesalius, Galen, Aristotle?
8. Outline the different views as to the function of the heart up to the time of Harvey.
9. How did Harvey prove that there was a circulation of the blood? What evidence was lacking from his demonstration? By whom was the evidence supplied?
10. How does a magnifying glass work? Explain the principle of the compound microscope.
11. Discuss briefly the work of Malpighi, Swammerdam, and Leeuwenhoek.
12. List some of the benefits to mankind which have resulted from the study of biology.

Suggestions for Further Reading

Locy, William A., *The Story of Biology*, Garden City Publishing Company, Inc., Garden City, N. Y., 1934.

CHAPTER 2

The General Characteristics of Living Things

It is usually easy to distinguish a living plant or animal from a stone or other lifeless object. Nevertheless, it is difficult to formulate a definition of life in exact terms. Before discussing the features which, in general, distinguish living from nonliving things, it will be well to have in mind specific examples of plants and animals to which the statements may be applied. For this purpose organisms of relatively simple structure and mode of life are chosen because their simplicity brings out more clearly the essential characteristics.

1. DESCRIPTION OF A SIMPLE PLANT: THE POND SCUM, *SPIROGYRA*

Most people have noticed at one time or another a light green scum on the surface of a pond. This is usually due to the presence of microscopic plants. One of the commonest of these bears the scientific name *Spirogyra*.[1]

When examined with a hand lens the "scum" is found to be made up of long threadlike filaments (Fig. 2:1). Under the compound microscope a filament is seen to be composed of numerous small cylindrical bodies joined end to end. These bodies are called **cells** and they contain the living material or **protoplasm** of the plant. Each cell is surrounded by a **cell wall** and the cell walls at the ends of the cylinders form the partitions between the separate cells (Fig. 2:2). The cell wall, although formed by the protoplasm, is not part of the living material since it does not take part in any of the vital activities of the cell. The actual living material or protoplasm lies inside the cell wall and forms what is called the **protoplast.** Bounding the protoplast and forming part of it is a very delicate membrane, the **plasma membrane.** So delicate is this membrane that it cannot actually be seen by the highest powers of the microscope. Its presence can be demonstrated, however, by causing the protoplast to shrink within the cell wall. Most of the protoplasm lies directly under the plasma membrane which is closely applied to the cell wall so that the greater part of the interior of the protoplast is occupied by a large **vacuole.** This vacuole contains a liquid, the **cell sap,** which should probably not be regarded as living material although it is included in the protoplast.

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[1] This is the name of the genus to which the plant belongs. Generic names are spelled with a capital letter and in this book are printed in italics. When so printed and spelled each should be used as the name of a group of organisms and not as that of an individual organism. When an individual of the group is intended the generic name may be used as an English noun in the singular, spelled with a small letter, and printed in ordinary type.

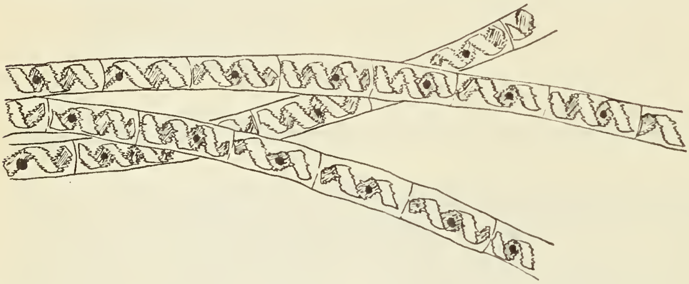

Fig. 2:1 *Spirogyra.* A general view showing parts of three filaments.

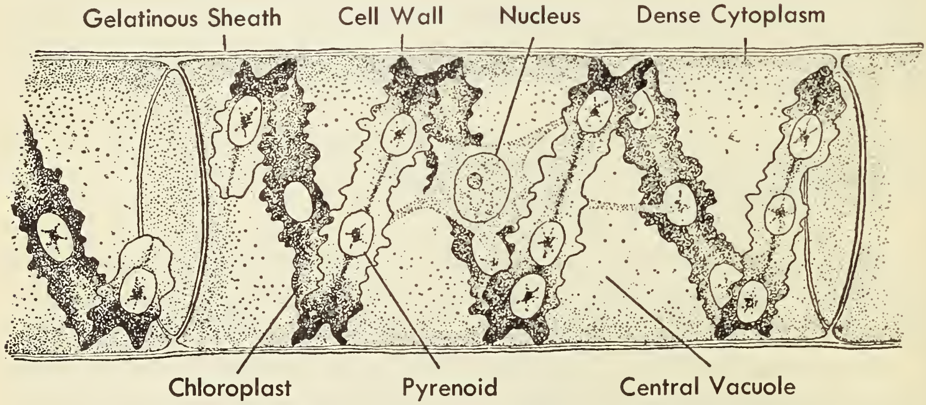

Fig. 2:2 One of the cells from a filament of *Spirogyra* highly magnified. After Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

Suspended near the center of the protoplast by strands of protoplasm extending to the periphery is an ovoid mass of protoplasm containing a spherical, highly refractive body called the **nucleus.** The nucleus is an essential part of the protoplast. Without it the cell cannot continue to carry on all of its vital functions.

The green color of *Spirogyra* is due to a mixture of substances to which the general term **chlorophyll** is applied. The chlorophyll is contained in a ribbon-shaped mass of protoplasm called a **chloroplast.** In the chloroplast are numerous small spherical bodies called **pyrenoids** which are centers of starch formation. The spiral form of the chloroplast is the reason for the name *Spirogyra.*

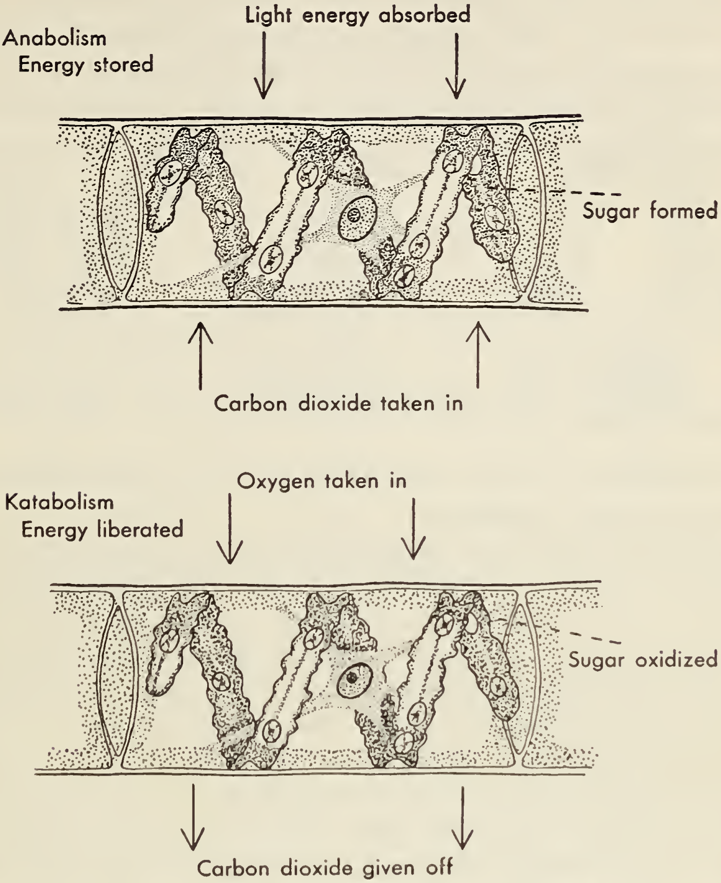

Fig. 2:3 *Spirogyra.* Diagram of metabolism. Above, anabolism; below, katabolism.

The activities of the plant include growth, which involves the manufacture of the materials needed to form new cells; movement and arrangement of the manufactured materials to form parts of the cells; and, under certain circumstances, movement of the protoplasm within the cell walls. To carry on these activities the plant requires energy. The energy is received in the form of sunlight, which is absorbed by the chlorophyll in the chloroplast. In the chloroplast the light energy is converted into chemical energy in the form of sugar. This process is called **photosynthesis.** The raw materials for the formation of the sugar consist of the gas carbon dioxide and water. The carbon dioxide and water diffuse into the protoplasm and into the chloroplast from the surrounding water (Fig. 2:3). The sugar is frequently converted into starch by the plant. The starch is practically insoluble and is deposited in the cells in the form of granules. In this form the material can be stored in the plant, to be later reconverted into sugar when needed. From the sugar and from the simpler chemical compounds (inorganic salts) which enter the protoplast directly from the water are formed the various substances which the plant uses to build up its body. The green plant is thus able to manufacture its own food materials, and in this respect it is independent of other organisms.

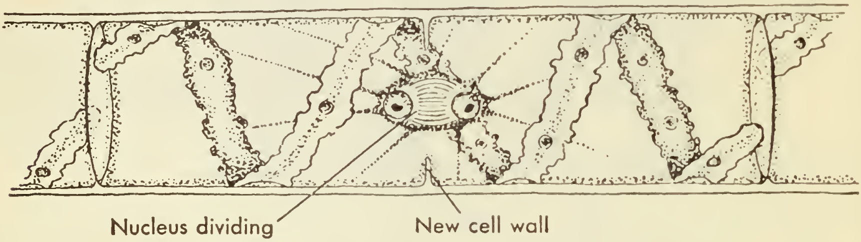

Fig. 2:4 A cell from a *Spirogyra* filament in process of division. After Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

Besides being a step in the formation of the more complicated chemical compounds needed by the protoplasm, sugar also acts to keep the vital processes of the plant going. In doing this it acts much in the same way that coal acts in a steam engine or gasoline in a motor. By combining with oxygen the sugar makes available to the plant the energy which was absorbed from the sun in its formation. Two processes are involved: an exchange of gases and an oxidation. The oxidation, i.e., the combination with oxygen, occurs in the protoplasts and, unlike the burning of coal, is accompanied by only a slight rise in temperature. The exchange of gases occurs through the plasma membranes of the cells. Together these two processes constitute **respiration.**[1] In the green plant during the day respiration is masked by photosynthesis, since in this latter process carbon dioxide is taken in and oxygen is given off, as the latter is usually formed in excess of that required for respiration. During the night, or when the plant is deprived of light, photosynthesis ceases. Respiration is then easily demonstrated by showing that carbon dioxide is given off.

The filaments grow in length by **cell division.** The nucleus divides first, and this is followed by the division of the entire protoplast and the formation of a new transverse wall separating the two daughter cells (Fig. 2:4).

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[1] This is the sense in which the term is usually used by biologists. By the earlier biologists the term was restricted to the exchange of gases. In medical literature it usually means breathing, i.e., taking air into and passing air out of the lungs.

When a filament of *Spirogyra* is torn in two by an aquatic insect or other animal, as often happens, each part continues to grow. This is probably the usual method by which the number of filaments is increased during the favorable summer season.

At certain times, however, especially in spring or autumn, **sexual reproduction** occurs. Two filaments become arranged parallel to each other. Small knoblike projections grow out from the cells and join, forming tubes that unite the cells of one filament with those of the other (Fig. 2:5). These tubes which place the cells in communication are called **conjugation tubes.** In this stage the filaments have the appearance of a miniature ladder, the conjugation tubes occupying the place of rungs. The protoplasts of the cells which have been put into communication by the conjugation tubes withdraw from the cell walls and shrink into rounded masses. One of the protoplasts begins the shrinking process in advance of the other and this protoplast migrates through the conjugation tube to join and fuse with its partner in the opposite cell. The fusion of the cells is followed by a fusion of their nuclei. The fusion of the nuclei is called **fertilization.** The single cell formed by the fusion of the two cells is called a **zygote.** Each of the two cells which fuse to form the zygote is called a **gamete.** In *Spirogyra* the gametes, although alike in structure, differ in their behavior. The gamete which migrates from one filament to the other is called the **male gamete.** The gamete which remains in its own filament is called a **female gamete.**

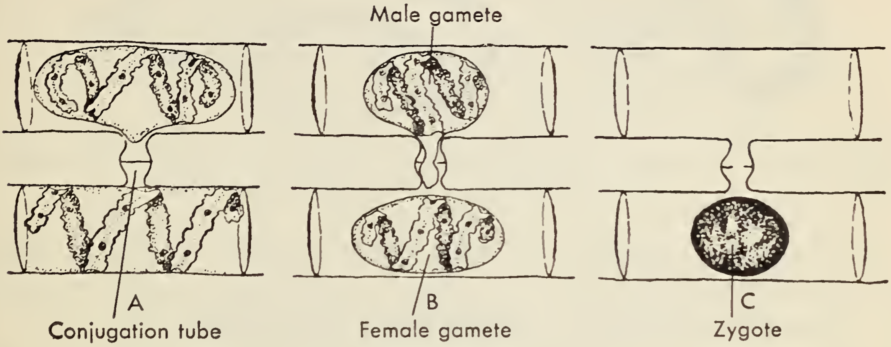


Fig. 2:5 Sexual reproduction in *Spirogyra.* A, formation of conjugation tubes and rounding of male gamete; B, migration of male gamete through conjugation tube; C, zygote forming zygospore. After Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The zygote forms a new resistant cell wall around itself inside the cell wall of the old filament and becomes a **zygospore.** After conjugation the filaments sink to the bottom of the pool and gradually disintegrate, leaving the zygospores. A period of weeks or months may intervene before **germination** (Fig. 2:6). When this occurs the outer resistant portion of the cell wall is broken and the protoplasm of the zygospore sends out a cylindrical process covered by a thin cell wall. Within this process the structure of a typical cell of *Spirogyra* appears. Cell division then occurs and a new filament is formed.

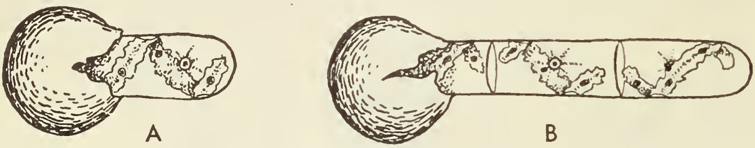


Fig. 2:6 *Spirogyra.* Germination of zygospore of *Spirogyra.* A, beginning of germination; B, cell division has occurred and the filament is beginning to elongate. After Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The formation of zygotes and the formation of spores are both methods of **reproduction.** The process by which zygotes are formed, involving the fusion of two gametes, is called **sexual reproduction.**

2. DESCRIPTION OF A SIMPLE ANIMAL: *HYDRA*

The small fresh-water animal called *Hydra*, for which there is no common name, is found in ponds all over the world. Several different species occur but they do not differ greatly from each other and we need not concern ourselves with the differences. The animal is small, rarely being more than a quarter of an inch in length when extended (Fig. 2:7). Its body is then roughly cylindrical in shape and quite slender, but when irritated it may contract into a rounded mass. One end, called the **foot,** is usually attached to an aquatic plant or some other object in the water. From the other end six to ten long slender **tentacles** project. The tentacles surround a conical raised portion, called the **hypostome,** in the center of which is the **mouth**

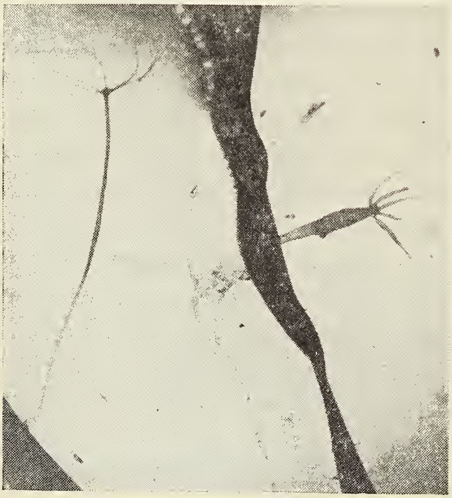
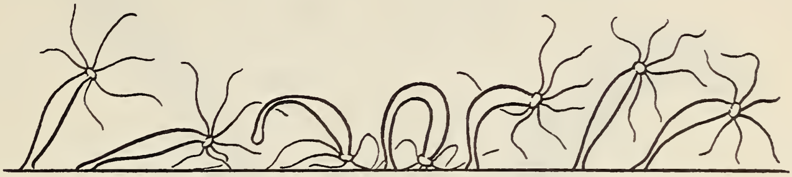


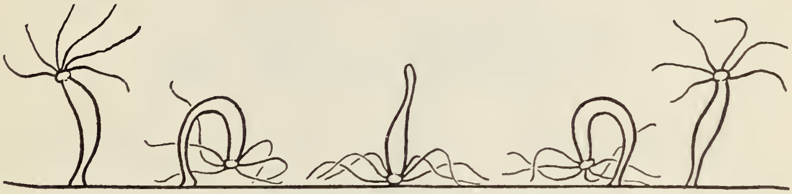
Fig. 2:7 *Hydra* attached to the leaves of a water plant. The hydra on the left is extended. That on the right is somewhat contracted and shows a small bud. Photograph by J. W. Mavor.

opening. The tentacles are usually seen sweeping through the water in search of the microscopic animals and plants on which the hydra feeds.

There are no eyes, ears, or other organs of special sense, but the animal is sensitive to touch and to chemical stimuli, and it also reacts to light, moving toward moderate light and away from bright light. *Hydra* has a number of different methods of **locomotion.** In one method the foot may glide over the substratum or surface of the plant or other object to which the animal is attached. In another method the movement is like that of a measuring worm; the body is bent over and the tentacles are applied to the substratum, after which the foot is detached and moved along toward the tentacles which are then moved forward and the process repeated (Fig. 2:8). In still another method the animal makes a series of extremely slow somersaults. The tentacles are attached to the substratum as in the case of the previous method, but the foot makes a complete semicircle and comes down in advance of the tentacles.



A. Locomotion like that of a measuring worm.



B. Locomotion by a series of somersaults.

Fig. 2:8 Locomotion in *Hydra.* After L. Jammes, *Zoölogie practique*, Masson et Cie., Paris.

The mouth opening leads into a relatively large cavity which fills the whole of the interior of the animal. This is termed the **gastrovascular cavity** (Gr. *gaster*, a stomach + *vasculum*, a vessel).[1] Into it are passed the small animals and plants which serve as food. They are there digested and the digested materials are absorbed by the cells of the hydra. The undigested materials are passed out at the mouth.

Hydra is so small and transparent that the entire animal can be placed in water under the compound microscope and the individual cells observed. However, the study of cells can be pursued to greater advantage on prepared sections of the animal. Such **sections** can be cut through the animal either in, or parallel to, its longitudinal axis, i.e., lengthwise, or transversely at right angles to the longitudinal axis, i.e., crosswise. For laboratory study transverse sections are generally used. For the purpose of the present description a diagrammatic longitudinal section will be most instructive (Fig. 2:9). The method by which such sections are prepared is described in more detail in Chap. 4. Here it will be sufficient to state that the tissue is hardened, differentially colored, and cut into

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[1] Also called the **coelenteron** (Gr. *coilos*, hollow + *enteron*, intestine).

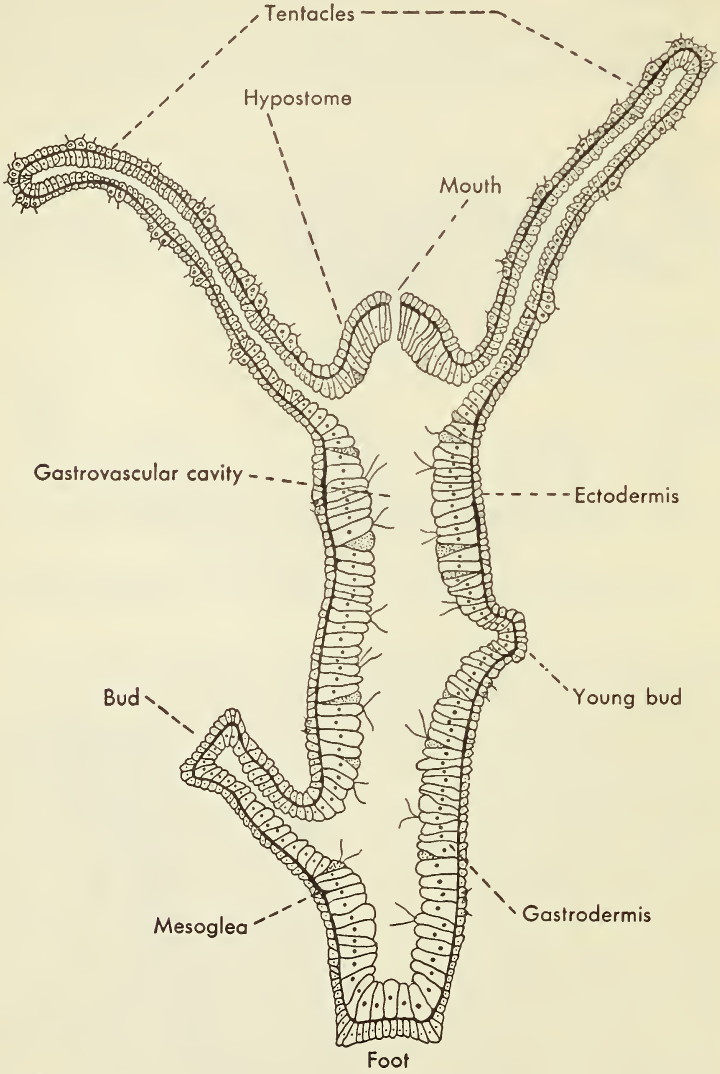

Fig. 2:9 *Hydra.* Semidiagrammatic longitudinal section of adult individual showing two buds.

very thin slices. Such sections reveal that the body of *Hydra* consists of two layers of cells surrounding the gastrovascular cavity. The outer layer of cells which is everywhere in contact with the water is called the **epidermis** (Gr. *epi*, over + *derma*, covering or skin), and the layer which lines the gastrovascular cavity the **gastrodermis** (Gr. *gaster*, *gastros*, stomach).[1] The epidermis is separated from the gastrodermis by a layer of jelly called the **mesoglea** (Fig. 2:10). Some of the epidermal cells develop **contractile processes** at their inner ends while others are differentiated into **nerve cells** which transmit nervous impulses from one part of the body to another. The cells of the gastrodermis also bear contractile processes and some of them are also differentiated into nerve cells. All of these cell processes lie against or in the mesoglea. Some of the larger gastrodermal cells carry long whiplike processes, called **flagella,** which serve to create currents in the fluid contents of the gastrovascular cavity. The nerve cells and the contractile processes in the epidermis and the gastrodermis make possible the coordinated movements

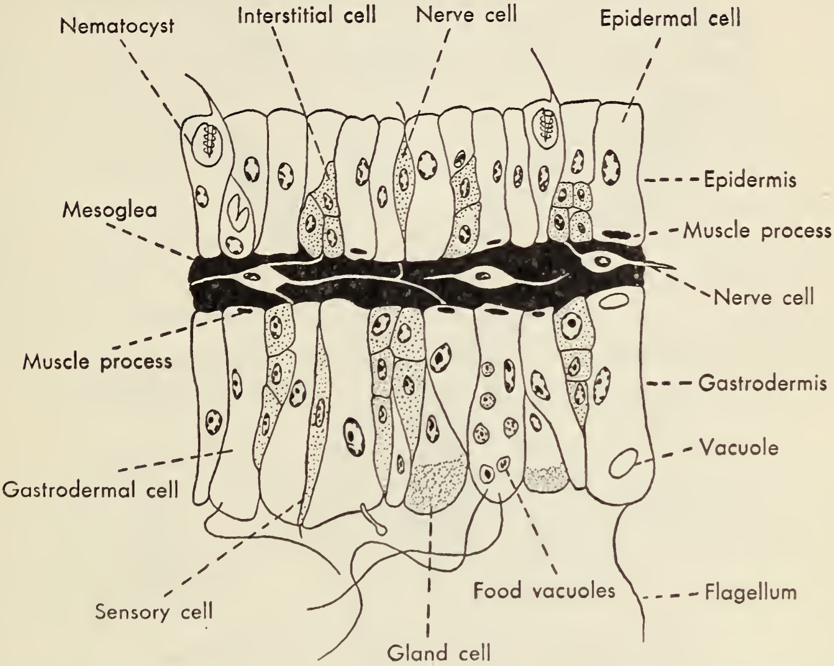

Fig. 2:10 *Hydra.* Cellular structure in body wall. Mesoglea is shown as black.

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[1] Some authors use **ectoderm** (Gr. *ectos*, outside) and **endoderm** (Gr. *endon*, within) for the outer and inner layers of *Hydra* and similar animals, but it is perhaps better to preserve these terms for embryos, and to reserve epidermis and gastrodermis for the layers in an adult animal such as *Hydra*.

of the body of the animal. Other specialized cells occur in the ectoderm.[1]

Unlike the plant described in the previous section, *Hydra* is unable to manufacture its own food materials. For these materials it is dependent on the bodies of the other animals and plants on which it feeds. The method of feeding has already been indicated. The small animal or plant is taken in through the mouth opening into the gastrovascular cavity. There **digestion** occurs, i.e., much of the material of which the small animal or plant is composed is made soluble in water by the action of digestive juices secreted into the gastrovascular cavity from cells in the gastrodermis (Fig. 2:11). *Hydra* is able to use for food only those materials which can be made soluble, since only soluble substances can pass through the plasma membranes of its cells and become incorporated in its protoplasm. The insoluble substances and the substances not absorbed into the cells of the hydra are extruded through the mouth opening. Small pieces of partially digested animals or plants may be engulfed by gastrodermal cells, to be digested in vacuoles within the cells. The

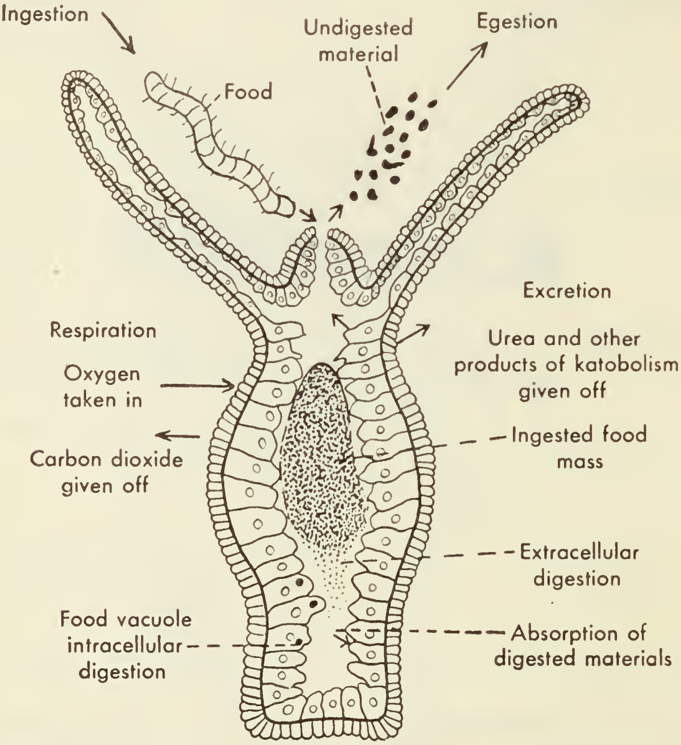

Fig. 2:11 *Hydra.* Diagram showing metabolism.

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[1] See Chap. 19.

material in the gastrovascular cavity is moved about by the flagella of the gastrodermal cells and by contractions of the body. In this way **distribution** of the food materials to all parts of the gastrodermis occurs. The cells of the epidermis obtain their food materials from the cells of the gastrodermis. Although *Hydra* obtains its food materials in part ready made, nevertheless, energy is needed to build them up into the specific substances which compose its protoplasm.

Just as the plant described in the previous section was found to require energy to carry on its vital processes, so *Hydra* requires energy to carry on its activities — which include movement, secretion of digestive juices, and the building up of its tissues. This energy it obtains through **respiration,** i.e., through the oxidation of food materials. Oxygen is absorbed through the entire surface of the body, there being no special respiratory organs. The oxidation occurs within the cells. Other substances besides carbon dioxide and water result from the process. In plants such waste substances occur usually only in small quantities, but in animals they occur in larger quantities and must be passed out by a process of **excretion.** The most important of these substances is **urea.** In the higher animals urea is excreted by the kidneys. In *Hydra* it passes, like the carbon dioxide, directly from the cells into the surrounding water.

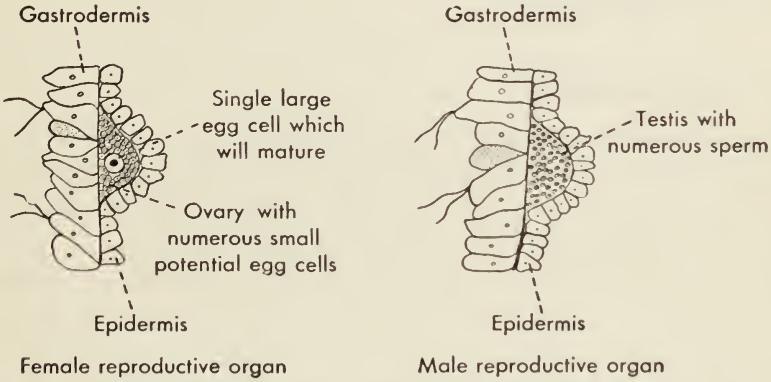
Gastrodermis
Single large egg cell which will mature
Ovary with numerous small potential egg cells
Epidermis
Female reproductive organ
Gastrodermis
Testis with numerous sperm
Epidermis
Male reproductive organ

Fig. 2:12 *Hydra.* Male and female reproductive organs, semidiagrammatic.

Both sexual and asexual reproduction occur in *Hydra.* The commonest method of **asexual reproduction** is by budding (Fig. 2:9). **Buds** arise on the sides of the body. When a bud is being formed, the epidermis and gastrodermis of the parent grow out to form a projection into which the gastrovascular cavity extends. A mouth and tentacles are then formed, after which the bud may become detached from its parent and carry on an independent existence. **Longitudinal** or **transverse division** of the whole animal into approximately equal parts also occurs, but rarely.

In **sexual reproduction** the **gametes,** or sex cells, are developed in special organs called **testes** and **ovaries.** Male gametes or **sperms** develop in the testes. In each ovary a single **egg cell,** or female gamete, is developed (Fig. 2:12). The relatively large egg cell is ladened with food material and remains in the ovary. When mature the testes burst and the sperm are freed into the sea water. Each sperm is provided with a single long flagellum and swims about actively until it finds an unfertilized egg or dies. Since the development of testes and ovaries does not usually occur simultaneously in the same individual, the gametes which join in fertilization usually come from different individuals. The fertilized egg develops into a young hydra similar to its parents.

3. THE CHARACTERISTICS OF LIVING THINGS

We are now ready for a general consideration of the characteristics of living things. These will be considered under the headings organization, growth and differentiation, metabolism, response to changes in the environment, and reproduction.

A. ORGANIZATION

When we call a plant or an animal an **organism** we imply that it is organized, that is, that it consists of parts carrying out functions which are correlated and contribute toward the activities of the whole. Thus the filament of *Spirogyra* is composed of cells which carry out living processes, and each cell is organized into parts such as the chloroplast which manufactures sugar or the plasma membrane which determines what materials can enter or leave the protoplast. Or, taking *Hydra*, we find that here the body of the animal can be divided into such parts as the tentacles, mouth, and body wall, each of which has a different function, and further that there are a number of different kinds of cells, each kind with a different function. From the correlated activities of these parts there results an organism which in the first case is a plant called *Spirogyra* and in the second an animal called *Hydra*. As will become apparent in later chapters, the organization extends beyond the visible parts of the cell into the arrangement of the substances of which the cell is composed.

Higher in the scale of organization are the more familiar trees, shrubs, and herbs. Here the plant body may be regarded as composed of various **organs** performing different functions. Thus the root is an organ which holds the plant in the ground and absorbs water and mineral substances from the soil; the stem is an organ which supports the leaves and conducts materials from one part of the plant to another; while the leaves are organs which are concerned chiefly with the manufacture of sugar. In an animal such as a fish, bird, or mammal the scale of organization is yet higher, and organs performing related functions are grouped into **systems of organs.** Some of the systems are the skeletal system, or skeleton, made up of the various bones which form the framework; the muscular system, with its different muscles which are responsible for the movement of the body; the digestive system, including the mouth, esophagus, stomach, and intestine, in which food is digested and through the walls of which food substances are absorbed; the circulatory system, consisting of the heart and blood vessels, which contains the blood and circulates it through the body; the respiratory system, including the lungs and trachea, which brings oxygen to the blood and takes carbon dioxide away from it; the excretory system, which includes the kidneys and eliminates waste products; and the nervous system, consisting of the brain, spinal cord, and peripheral nerves, which largely controls and coordinates the activities of all the other systems and organs.

Also in these animals the organization is carried further and into the finest details. Thus organs are composed of **tissues,** and tissues are made up of cells. The cells which compose a tissue are similar in structure and are specialized to carry on a particular function. The term tissue is usually used to include not only the living cells but also structures produced by them and associated with them, such as the cell walls, the hard material of bone, and the fibers of tendons. Most organs contain a number of different kinds of tissues. Thus, for example, the heart, although a muscular organ and consisting largely of muscle tissue, contains connective tissue, blood (both in its cavities and in the blood vessels of its muscles), and nerve tissue, and is covered and lined with epithelial tissue.

All animals and plants consist of either a single cell or groups of **cells.**[1] In the case of large plants and animals the number of cells in an adult individual may reach many millions. An individual plant or animal usually starts its existence as a single cell.[2] This cell divides first into two parts to form two cells. Then each of these cells divides again into two, giving a total of four cells, each of which again divides, and so on. In cell division the nucleus always divides first and this is followed by the division of the cell.

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[1] There are a few exceptions which will be considered in later chapters.

[2] Exceptions occur in certain cases of asexual reproduction which will be referred to in later chapters.

As already indicated, organization may be defined as a systematic arrangement into parts such that each part may perform one or more functions contributing to the activities of the whole. It involves division of labor among the parts and their specialization to carry out that labor more effectively. The question arises whether organization is confined to living things. An automobile, it may be said, consists of various parts such as the steering gear, motor, and so on, which perform different but related functions and are comparable to the organs of an organism. The term may be applied to a town or city, which is said to be organized into departments, industries, and the like. These are, of course, organized bodies but we must not forget that they are products of human activity and that they thus owe their organization to a living thing. They are, in fact, like cell walls or sea shells, products of living things. The nearest approach to organization to be found in the inorganic world and unrelated to living things probably occurs in inorganic crystals like the snowflakes which form on a windowpane. Here there is a certain amount of structural organization but it would require a stretching of the imagination to assign functions to the structural units in order to carry through the comparison.

B. GROWTH AND DIFFERENTIATION

In the **development** of any organism two processes are usually involved. They are growth and differentiation. Growth appears as increase in size, differentiation as differences between the cells and tissues leading to specialization.

There is usually a limit to the size which any type of cell in an organism may normally attain. Once this **cell size** is reached, further growth is impossible unless the cell divides. After this has occurred the daughter cells may grow to a size approximating that of the parent cell. In general, large plants and large animals have large numbers of cells, rather than large cells. However, there is no definite general relationship between the size of an organism and the size of its cells; the blood cells of a frog are larger than the blood cells of an elephant or a man.

The **growth** of a cell involves more than mere increase in size. While it is growing it continues its other vital activities and maintains the organization which makes possible its activities. Although the proportions of the different parts may change, each continues to carry on its function or functions harmoniously and in coordination with the other parts. This would not be possible if the new materials were simply added on the outside as occurs when a crystal "grows," or even if they were deposited in masses in the interior. The new materials to be added are distributed in the living protoplasm and become a part of its finely organized structure. This kind of growth is called **growth by intussusception** (from the Latin: *intus*, within + *suscipere*, to take up) to distinguish it from increase in size by the mere addition of material to the outside, which occurs in crystals and which is called **growth by accretion.**

Cell differentiation will be better understood after the detailed structure of cells and the development of embryos have been discussed in later chapters. Here only a brief general statement can be made. In the early stages of an embryo the cells are usually much alike, and only after the different organs have begun to take form do the cells gradually take on the characteristics of cells of the different tissues, such as the conducting tissues of a plant or the muscular tissues of an animal.

It is worth while to pause for a moment and to try to imagine what happens in any living organism, a man for example, when growth and differentiation occur. Every organ continues to function and the individual cells of the different tissues continue their vital activities.

The heart as it grows keeps up its even rhythm without so much as missing a single beat. The lungs continue without intermission to take in air, and the oxygen in the air continues to be absorbed into the blood vessels. The muscles as they grow continue to respond to stimuli by contraction. The bones as they increase in size and strength continue their functions of support and protection. Similarly, in a giant tree, the stem and roots grow continually in length and thickness. Try to imagine an automobile or any man-made machine gradually increasing in size while continuing in operation.

C. METABOLISM

By **metabolism** (Gr. *meta*, beyond + *ballein*, to throw, meaning to change) is meant all of the chemical changes, including all of the chemical processes, which take place in a living thing. As outlined in the descriptions of *Spirogyra* and *Hydra*, some of these changes lead to the formation of the complex organic substances which actually make up the living protoplasm or are stored in it. These substances, which are mostly carbohydrates, fats, and proteins, will be discussed in detail in a later chapter. To that part of metabolism which consists of the building up of materials for use by the organism the term **anabolism** (Gr. *ana*, upwards + *ballein*, to throw) is applied.

Also included in metabolism are the processes in which materials are broken down either because they no longer serve a useful purpose or because, like sugar, they are used as a source of energy. To all of these processes the term **katabolism** (Gr. *kata*, downward + *ballein*, to throw) is applied. The oxidations which occur in respiration are an important part of katabolism.

The early students of living things thought that there was manifested in them a special kind of energy, or a "vital force," different from the forms of energy or the forces encountered in chemistry and physics. Efforts to locate or identify any such force have so far been negative. On the contrary it is possible to explain the energy changes in plants and animals on purely physical and chemical grounds.

Careful experiments have been carried out to determine whether the total amount of energy received by an animal (chiefly in the form of food and heat) is equal to the total amount of energy required by it to perform all of its activities, or, in other words, to determine whether it is necessary to assume some extra-physical source of energy. In these experiments the amount of energy received by the animal in the form of food and heat is accurately measured and at the same time the energy liberated in the form of movement and heat is determined. For measurements to be comparable the experiment must be done over a considerable period of time and under conditions in which the subject neither gains nor loses weight, i.e., neither stores up energy nor gives up stored energy. When these conditions are satisfied it is found that the debit and credit sides of the account balance; in other words, the amount of energy received is equal to the amount of energy given off within the limit of accuracy of the experiment, which is 1 or 2 per cent. These results show, always within the limits of experimental error, that from the point of view of the energy involved, the activities of animals, and probably also of plants, can be explained by applying purely physical and chemical principles.

No real parallel to metabolism is known to occur in the inorganic world. Although inorganic materials may be built up and more complex substances formed (as appears to be the case in the formation of rocks), and these materials may be broken down and oxidized (as also occurs in rocks), the processes when they occur in nonliving things are not organized as in the metabolism of animals and plants.

D. RESPONSE TO CHANGES IN THE ENVIRONMENT

Two features stand out in the relations of organisms to their environments. One, which is known as adaptation, is of a more or less permanent character and concerns the suitability of the structure of the body and the functioning of the organs to the particular conditions under which the organism lives. The other, known as irritability, involves the more or less immediate reactions of the organism to changes in the environment.

(1) ADAPTATION

In order to live successfully a plant or animal must fit its surroundings. The various parts and organs of its body must be able to carry out their functions under the conditions which the environment presents. Organisms tend on the one hand to seek out environments which are suited to their particular modes of life and characteristics, and on the other hand there is evidence that they may gradually become modified to suit a particular environment.

The different species of plants and animals differ from each other in their adaptations. Indeed it is probably more correct to say that the species differ because they are adapted to different modes of life and different conditions. In the living world structure and function go hand in hand and plants or animals even of the same species which have adopted different modes of life show structural differences. The adaptations of organisms may be grouped according to the vital activities with which they are concerned, as follows: capture and utilization of food, respiration, adjustment to physical and chemical surroundings, locomotion, protection against enemies, and reproduction.

An organism must be able either to utilize the food materials in its immediate surroundings or possess the means to search for and obtain those which it is able to utilize. A green plant can obtain all that it requires from the atmosphere and the soil. This it is able to do because of its leaves and roots. A horse can exist on grass because its teeth and jaws are adapted to grazing and its digestive system to that kind of diet. A hawk, on the other hand, is adapted to eat flesh by having long talons and a sharp beak to catch its prey.

A fish taken out of water soon dies. It becomes asphyxiated, for while its respiratory organs, consisting of mouth and gills, are adapted to take dissolved oxygen out of the water, they are unsuitable for absorbing oxygen from the air. Quite the reverse is the case with a man, for his lungs, although admirably adapted to breathe air, cease to function when filled with water. Respiratory adaptations also occur in many plants. The dark oval marks so conspicuous on the trunk and branches of the white birch surround respiratory openings called **lenticels** (Fig. 15:10) by which air can pass into the living cells which lie under the bark.

Life in water has necessitated many adaptations. Most marine animals are unable to live in fresh water. The first fishes presumably evolved in the sea. Later some of these took to fresh water. When they did so the species had to become adapted to the lack of salt in the fresh water. Most plants are very sensitive to water. Some plants live only in water, others only on land in humid climate, while others require a dry climate. These different requirements are reflected in the structure of their leaves and roots.

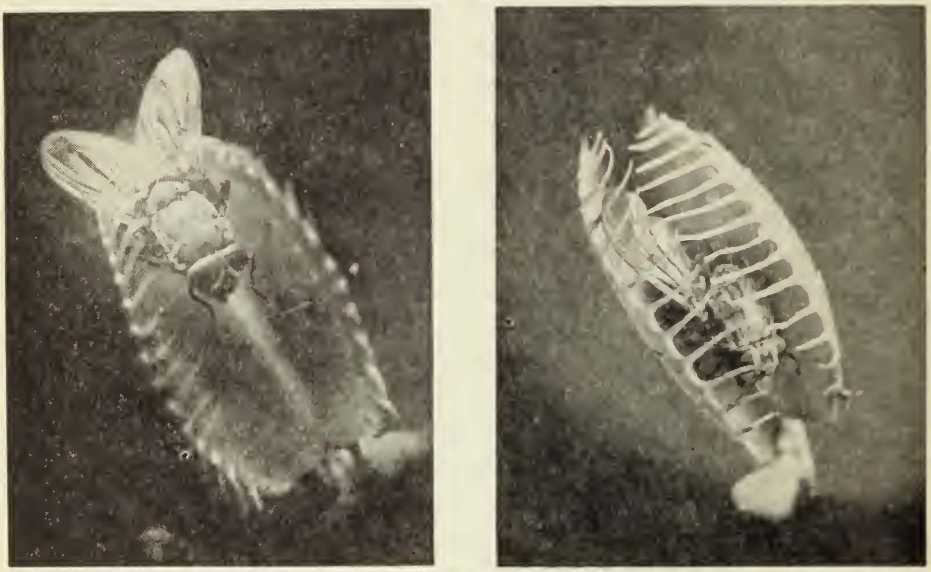

Fig. 2:13 A Venus's-flytrap (*Dionaea*) taken in the act of catching and digesting a fly. Sequence of photographs reproduced by permission of General Biological Supply House, Inc.

Locomotion has brought about many of the most conspicuous of animal adaptations. Vertebrates which live in water, whether they be fishes, turtles, birds like the penguin, or mammals like the whale, tend to have appendages which are finlike in external appearance and in function, although in their internal structure they conform to that of the group to which they belong. In flying vertebrates, whether they be flying fishes, flying reptiles, birds, or bats (which are mammals), the fore limbs take the form of wings. Running animals have long slender legs, as in the ostrich, the horse, and the antelope. The list could be extended with many other examples of adaptation in the locomotor organs of animals.

Some of the greatest hazards which living things encounter are changes in their physical environment. This is specially the case in organisms which live on land, or those which live on the seashore between low and high tide, or in bodies of fresh water which dry up during certain seasons. Many animals protect themselves from changes in the environment (and from their enemies) by burrowing; others develop shells, scales, feathers, or hair.

Nearly every plant or animal has its enemies. "Enemies" is perhaps not a very apt word in this case since the destruction of one wild animal or plant by another is rarely, if ever, accompanied by the feelings which we associate with the word "enemy." An organism's enemies are those animals or plants which feed upon it. To protect themselves from being eaten, many plants have developed thorns, offensive odors or tastes, and, in some cases, poisons. For similar reasons, animals have developed shells and scales, spines, and other protective armor. A curious kind of adaptation is the protective coloring of many animals, which may make them almost indistinguishable from their surroundings.

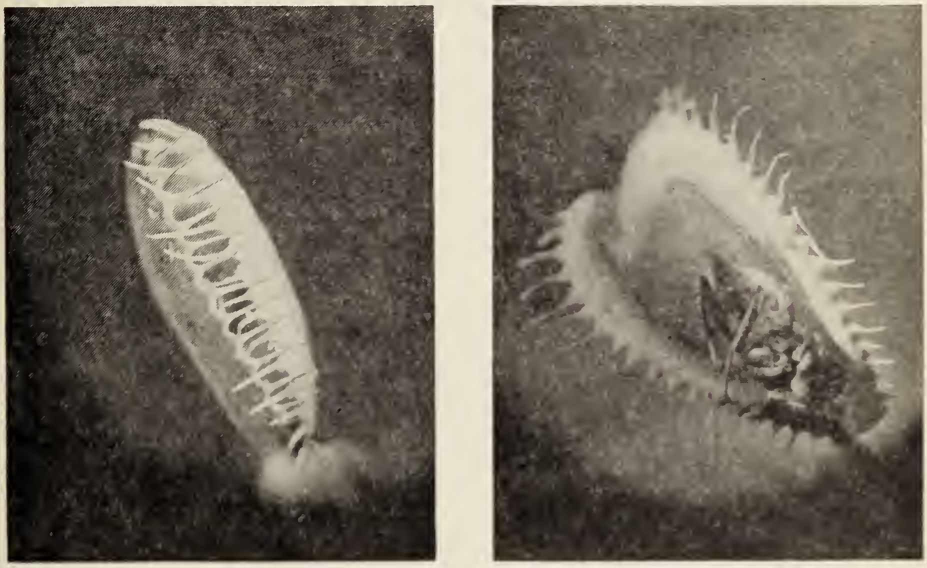

Fig. 2:13 *Continued.*

(2) IRRITABILITY

Irritability is the capacity to respond to a stimulus. A **stimulus** is a more or less rapid change in some feature of the environment, such as a change in the intensity or direction of the light, in the temperature, in the pressure on the surface of the body, or in the chemical composition of the atmosphere or water in which the plant or animal lives. Thus the specialized leaves of the plant named the Venus's-flytrap, when touched by an insect, come together and enclose it in a trap (Fig. 2:13). The stimulus does not provide the energy for the reaction: it merely starts it off as a trigger starts the explosion in a gun. To take another example: A blow which knocked a man down would not, according to this definition, be a stimulus, since it provided the energy for the movement. On the other hand, the slight tap just under the knee which makes any normal individual respond with a violent kick, known as the knee jerk, is a true stimulus.

Under the stimulus of **light,** vast numbers of insects may collect about a street lamp on a summer night. Many plants turn toward the direction of greatest light intensity (Fig. 16:6), and if this direction changes the plant will continue to turn toward it. Some of the reactions of *Hydra* have already been mentioned. Earthworms and many other animals shun the light of day and come out of their hiding places only at night. The above plants and animals are without special organs for receiving light stimuli, but many animals have developed special organs, usually referred to as eyes, for the better reception of light. Man is particularly dependent upon light stimuli for information regarding the external world, and his movements are often largely dependent upon what he sees.

Changes in **temperature** affect all organisms. Plants are particularly sensitive to such changes. With the warmth of spring seeds germinate and buds burst open. The coming of the cold winter stimulates earthworms to burrow below the frost line and bears to seek out their dens, while the warmth of spring stimulates them to come out again. In our own skin are special sense organs for detecting changes in temperature, and the hand or foot is quickly withdrawn from a hot object.

Response to **pressure** is shown by almost all living things. It is well seen in climbing plants which wind their stems round the trunks of trees or attach their tendrils to rocks and stones. Touch a hydra and it contracts into a rounded mass. Special organs, such as feelers and tentacles, have been developed by many animals, notably those which live and are active in the dark.

The response to **sound** is in reality a refinement of the response to pressure, since sound waves are actually waves of increasing and decreasing pressure. The stimulus of sound often causes animals to move away. The barking of dogs, the songs and calls of birds, and the chirping of insects act as stimuli to their fellows and serve like a primitive form of speech to warn of danger or tell of the presence of food. Special organs for detecting sounds occur in many insects and most vertebrates.

The roots of plants are especially sensitive to **chemical substances** in their surrounding, turning and growing toward some and away from other substances. Responses to chemical stimuli are often associated with feeding. Some confusion exists in the use of the words "smell" and "taste." In general "smell" is used when the substance comes to the animal in the form of a vapor or minute particles, while "taste" is used when the substance comes to the animal either as a liquid or dissolved in a liquid; but frequently the distinction is not clear, since a substance to act as a chemical stimulus must usually be dissolved before it can affect protoplasm. Some animals have the chemical sense widely distributed over the surface of their bodies, as in *Hydra*. Chemical stimuli are of great importance in the internal adjustment of the body. Thus the rate of breathing is largely controlled by the amount of carbon dioxide in the blood.

The **response** of an organism to a stimulus differs depending on the stimulus and condition of the organism. Movement has already been mentioned many times. Glands respond by pouring out their secretions. Food taken into the mouth, or even the odor of food, causes a flow of saliva; and as food passes down the alimentary tract various glands respond with other secretions or "juices" which bring about the digestion of the various food substances.

Through the mechanism of stimulus and response, with the stimulus acting directly on the living material or through the intermediary of nerves or internal secretions, the activities of every organ are coordinated and controlled by the activities of every other organ. This offers a partial explanation of why the organism behaves as a unit and not as a mere collection of parts.

To find a parallel in the inorganic world to the response to stimuli so characteristic of organisms, one must turn either to man-made machines or to those physical or chemical reactions which depend upon a more or less sudden release of energy in response to a slight change, known as trigger reactions. In the case of the machine it should be noted that, as explained in the section on organization, we eventually come back to the human organism. An example of a trigger reaction occurs when a charge of dynamite is fired by a fuse. The chemical energy present in the dynamite is suddenly set off. Here, however, the reaction, which is the explosion, simply goes to an end. The dynamite as such disappears and there is no return to the original condition. Animals and plants have the power of automatically restoring themselves to their original condition after a response.

E. HOW ORGANISMS ARISE

It is common knowledge that plants and animals reproduce their kind. But it was not always known that living things arise only from other previously existing, living things.

(1) CONTINUITY OF LIFE

There is a famous quotation from Aristotle (384–322 B.C.) which describes how many insects are "not derived from living parentage, but are generated spontaneously, some out of dew falling on leaves ordinarily in springtime, but not seldom in winter when there has been a stretch of fair weather and southerly winds." Even as late as the seventeenth century there were current many fantastic accounts of spontaneous generation, and today, from time to time, one sees in the daily press accounts of rains of frogs and toads. Many schoolboys believe that horsehairs falling in water give rise to worms, and housewives not uncommonly affirm that maggots arise directly from decaying meat.

That maggots do not arise spontaneously in meat but from eggs laid on it was proved by Francesco Redi in 1668. The experiment has already been referred to briefly in Chap. 1, sec. 1. Redi placed three jars containing fresh meat near a window. One of the jars was left uncovered, a second was covered with gauze, and the third with parchment. In each of the jars the meat decayed but maggots developed only in the jar which was left uncovered. Eggs were laid on the gauze covering the second jar but no eggs were laid on the parchment. Redi concluded that since maggots developed only where the flies had free access to the meat, they could come only from eggs laid by the flies. Further he argued that since the odor of the decaying meat could pass through the gauze but did not pass through the parchment, the flies when about to lay their eggs were attracted by the odor of the decaying meat.

That microorganisms such as bacteria do not arise spontaneously was shown by **Louis Pasteur**. Bacteria are frequently grown or "cultivated" in beef broth, which is really nothing more than what is served at the dinner table under the name of consommé. In making it, water, in which beef has been boiled or to which beef juice has been added, is filtered to obtain a clear liquid. It is common knowledge that if this liquid is kept for a few days at ordinary room temperature it will putrefy. The putrefaction causes the liquid to become cloudy and to give off an offensive odor. It was known in Pasteur's time that these changes were always accompanied by the presence of numerous bacteria and the belief was current that the bacteria arose spontaneously in the broth. Pasteur disproved this in a famous experiment. He boiled beef broth in a glass vessel which was open to the outside air only through a long, fine, curved tube, which was bent in the form of a U. When the vessel and its contents were allowed to cool after boiling, a small portion of the liquid condensed in the U and formed a seal preventing the access to the liquid of any particles carried in the air (Fig. 2:14). Pasteur found that even after a long time no evidence of bacteria or other growth appeared in the boiled broth. In order to prove that boiling in a partly closed glass vessel did not make the broth unfit for the growth of bacteria, Pasteur broke off the fine glass tube giving the air and its contained dust access to the broth and found that bacterial putrefaction set in. In performing the experiment today we would use a plug of absorbent cotton in place of the fine tube. We now know that bacteria are carried in the air in the form of spores which germinate when provided with the proper conditions, for example, when they fall into beef broth.

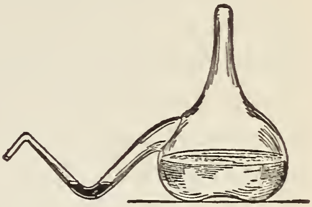

Fig. 2:14 Pasteur's experiment disproving the spontaneous generation of the bacteria of fermentation. From L. L. Woodruff, *Animal Biology*, The Macmillan Company.

These experiments, which are negative so far as spontaneous generation is concerned, have nevertheless been of the greatest importance to science. They laid the foundation for all subsequent work in bacteriology and its related sciences. However, there always remains the possibility that some condition not present in the experiment might give rise to some primitive form of life. Indeed it is generally believed that life must have arisen somewhere at some time and a number of theories have been advanced to account for its origin.

(2) REPRODUCTION

It is obvious that if any species is to maintain its existence it must possess the means of replacing by new individuals those lost by death. As was illustrated in the case of *Hydra* and *Spirogyra* this process of forming new individuals, called **reproduction,** takes two forms known as asexual and sexual reproduction.

In **asexual reproduction,** which is the simpler, the new individual arises from a part of an older individual. The part may be a single cell, as in the case of the spores formed on the under side of fern leaves, a considerable part of a plant or animal, as in the case of the tubers formed by the potato, or the whole organism may divide into two or more equal parts, as is sometimes the case in the lower plants and animals and has already been referred to in *Hydra.*

In **sexual reproduction** two cells unite to form a single cell and from the single cell a new individual develops. In most plants and animals the reproductive cells are differentiated into sperm and eggs as in *Hydra.* Sperm are usually minute, actively motile cells, while the corresponding egg cells are usually nonmotile and much larger, due to the storage of food materials for the new individual. Generally the eggs and sperm are formed in different individuals. An individual which produces sperm is called a male, while an individual which produces eggs is called a female.

One may ask, Why this complicated sexual process when new individuals can be produced simply and abundantly by asexual reproduction? The answer is to be found in the fact that the sexual method of reproduction ensures something more than mere propagation. In the case of the asexual method the individuals that are formed are exactly like the parent individual, being, in fact, only pieces of it which have separated off and undertaken an independent existence. In the case of the sexual method the offspring is an essentially new individual, having arisen from the union of two cells from two different parents, both of which have transferred characters to it through these cells. In providing new individuals, usually different from either of the parents, sexual reproduction provides the raw material for evolution. Exactly how sexual reproduction leads to the production of new individuals is discussed in Chap. 37, "The Physical Basis of Heredity."

Topical Outline of Chapter 2

1. Description of a simple plant, the pond scum, *Spirogyra* 27
2. Description of a simple animal, *Hydra* 32
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   - A. Organization 38
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Questions

1. Develop the idea of organization and apply it to *Spirogyra* and *Hydra*.
2. In what respects does the growth of a plant like *Spirogyra* or an animal like *Hydra* differ from the growth of a crystal?
3. What part do the cells play in the growth and differentiation of an organism?
4. What processes are included in metabolism and what two forms does it take?

5. Discuss whether it is necessary to assume some extra-physical source for the energy utilized by plants and animals.
6. Give examples of adaptation based on your own observations of plants and animals.
7. Explain clearly what is meant by a stimulus, giving examples.
8. What is meant by the continuity of life? Discuss the experimental evidence for this.
9. What two forms does the process of reproduction take in plants and animals and how do they differ in (*a*) method, (*b*) results?

CHAPTER 3

The Classification of Plants and Animals

From the earliest times man has been impressed by the multitude of living things and by their great variety. Why should life take on so many forms? Why should there be so many different kinds of trees, flowers, insects, fishes, and birds? The answer is to be found in the adaptation of each organism to the particular conditions of its environment. Organisms differ in size, color, shape, internal structure, and mode of life because their environments are different; and to a certain extent it may be said that they live in different environments because they differ in size, color, shape, internal structure, and mode of life. The variety of external and internal structure which organisms show is due to the variety of conditions which exist in the world and to the way in which each organism becomes adapted to the special conditions which it encounters. Some of these special conditions may be due to other organisms — for example, those upon which it feeds or those which feed upon it.

1. STRUCTURE AND ADAPTATION

An organism may be regarded as showing a certain **structural** type. Thus a frog (Fig. 27:1) shows the structural type of a backboned animal or vertebrate, and a lobster (Fig. 23:1) or a bee (Fig. 23:20) shows the structural type of an arthropod. This does not imply that it was built from a blueprint like a modern house or automobile, but rather that its organs, tissues, and cells show certain structural relationships which are found not only in the particular species but in other similar species, indeed in all the organisms which conform to the type. Again, there is the type of the seed-bearing plants with their roots, stem, leaves, flowers, and seed; the structural type of the ferns and their relatives with fronds, simpler stems, and spores borne on the fronds; and the simple type of many water plants which consist of aggregates of undifferentiated cells.

The structural type of the **vertebrates** (Fig. 26:1) involves, among other features, an internal skeleton consisting of a skull and vertebral column or backbone which serves as a framework to which muscles and ligaments are attached on the outside of the bones and as a protection for the brain and spinal cord; respiratory organs consisting of gills or lungs which are connected with the mouth through the pharynx; a digestive tract or alimentary canal including a stomach and intestine; a liver; kidneys; and a heart situated on the ventral or under side of the body. How the structure of these various organs is suited to the functions which they perform is discussed in the part of this text dealing with comparative anatomy.

Another type is that of the **jointed-legged animals** (phylum Arthropoda) which includes the lobster (Fig. 26:1). Here the skeleton takes the form of a hard outer covering, composed of a substance called chitin, which contains and protects the soft parts of the body. Parts of this chitinous covering, especially between the segments of the body and in the legs, are jointed to permit movement. In this type of animal the muscles are attached to the inside surfaces of the parts of the skeleton. With this type of skeleton is associated a certain type of nervous system which consists of a number of separate groups of nerve cells on the under side of the body, while the heart is found on the upper side.

The structure of a **mollusk,** such as the clam, is again different. Here the skeleton consists of a hard outer shell into which the animal may withdraw its soft body. The internal structure of this soft body again differs in the arrangement and structure of the separate organs from either of the two types above. In a **segmented worm** (Fig. 22:2), such as the earthworm, the body is divided into a series of segments, nearly every one of which is supplied with a nearly complete set of vegetative organs. In the **radiate** type seen in the starfish (Fig. 25:9) and its relatives the organs are arranged in the form of a five-pointed star and the locomotor organs consist of numerous peculiar tube feet which adhere by suction to foreign objects and pull the animal along. One of the simplest types involving more than a single cell is that of jellyfish (Fig. 19:5) and sea anemones (Fig. 19:7), which are scarcely more than sacs surrounding a digestive cavity.

The mere act of living imposes certain restrictions on the structure of organisms. Certain organs are essential and these organs must be located in the animal or plant in a position where they can carry out their functions. Thus the leaves of a plant must be exposed to the air and sun if they are effectively to carry on photosynthesis; and the roots, if they are to absorb water from the soil, must be in the ground. The digestive organs of an animal must be connected directly or indirectly with its mouth; respiratory organs must communicate with the air or water in which the animal lives; muscles must be connected with the structures they move; if there is a central nervous system it must be connected with the other organs of the body, both sensory and motor, and for its best functioning it must be protected from the direct effects of the environment.

Although there are over a million different species of plants and animals the number of fundamentally different types is probably not more than twenty. These fundamental types are used by biologists as a basis for the classification of plants and animals into major groups or **phyla** (singular, **phylum**).

When these major groups are studied in detail it is found that the fundamental type of structure differs in detail in particular cases, producing the characteristics of smaller groups and that these differences consist in the main of adaptations to the environment or mode of life of the particular group. The principle may be illustrated in the vertebrates. These backboned animals all conform to the same fundamental structural type. However, this differs in detail in the different groups of vertebrates which are recognized as fishes, amphibians, reptiles, birds, and mammals. In fishes the appendages take the form of fins which are adapted to locomotion in water. In mammals, which are typically terrestrial animals, the appendages take the form of legs adapted for walking and running. In birds, on the other hand, the fore limbs take the form of wings adapted for flight. In all of these groups there are typically two pairs of appendages, and the bones and muscles of the corresponding pairs conform to a certain fundamental plan of structure which is that of a vertebrate. Other differences between these groups, such as the shape of the body or the possession of scales, hair, or feathers, also suggest themselves as modifications of the general plan which is, however, always present in its main outlines. The differences may be of such a nature as to cause considerable variation from the type. Thus the respiratory organs of fishes are gills adapted for breathing in water, while those of mammals are lungs adapted for breathing air, and those of birds include, besides lungs, air sacs extending into various parts of the body, increasing their efficiency and making the animal lighter. Or, the modifications may be less fundamental, such as those which distinguish a mammal like a rabbit — which has large chisel-like front teeth for gnawing and a digestive system adapted to a vegetable diet — from a flesh-eating mammal like the cat, which has sharp claws and teeth adapted to catching its prey and the digestive system of a flesh eater.

Adaptation sometimes brings about external resemblances between animals which differ fundamentally in structure. A hummingbird and a sphinx moth look much alike as each hovers over a flower and sucks nectar. Yet the hummingbird is covered with feathers, has lungs, a true brain, and a spinal cord on the upper side of its body — in short has the structural plan of a backboned animal, while the sphinx moth has an external skeleton of chitin, breathes by means of numerous fine air tubes, has a central nervous system consisting of ganglia or solid groups of nerve cells on the under side of its body — in short the structural plan of an insect.

2. EVOLUTION

Science has been defined as the attempt to find order and reason in the universe. In the living world this attempt to find order and reason is expressed in the theory or, better, the principle, of evolution. It is the only principle yet advanced which satisfactorily accounts for the varied forms which life has taken on this globe. We are concerned at this stage merely with getting a clear idea of what the term "evolution" means, rather than with proving that it occurs. The evidences for the occurrence of evolution will be discussed in a later chapter after the necessary factual foundations have been laid. Unfortunately the human implications of the principle have overshadowed all others in the popular mind, and the term has come to mean for many laymen little more than the rather misleading idea that man was descended from a monkey. Consequently many otherwise intelligent people fail to appreciate its true significance. It will help toward a clearer understanding of the meaning of the term "evolution" if we endeavor for the moment to forget its human implications and try to be impartial and objective. Expressed in a simple way, evolution means only that everywhere in the universe, in the inanimate and the animate worlds, there exists a gradual and unending process of change leading to the continuous unfolding of new things, and that such new things, be they inanimate or animate, can arise only from things which preceded them. Viewed in this way evolution is really a long continued story — the story of a drama full of action, pathos, and tragedy. Important events in the drama were the birth of our sun as one of the children of a great spiral nebula, the forming of our little planet as a child of this sun, on it the birth of life awakened from lifeless inorganic matter by the radiant energy of its parent sun, and then millions of years after, the coming of the higher plants and animals, one form succeeding another, changing with the changing face of the earth and contributing its share to the great web of life which covers the planet.

Postponing for the present any discussion of the origin of life, we are

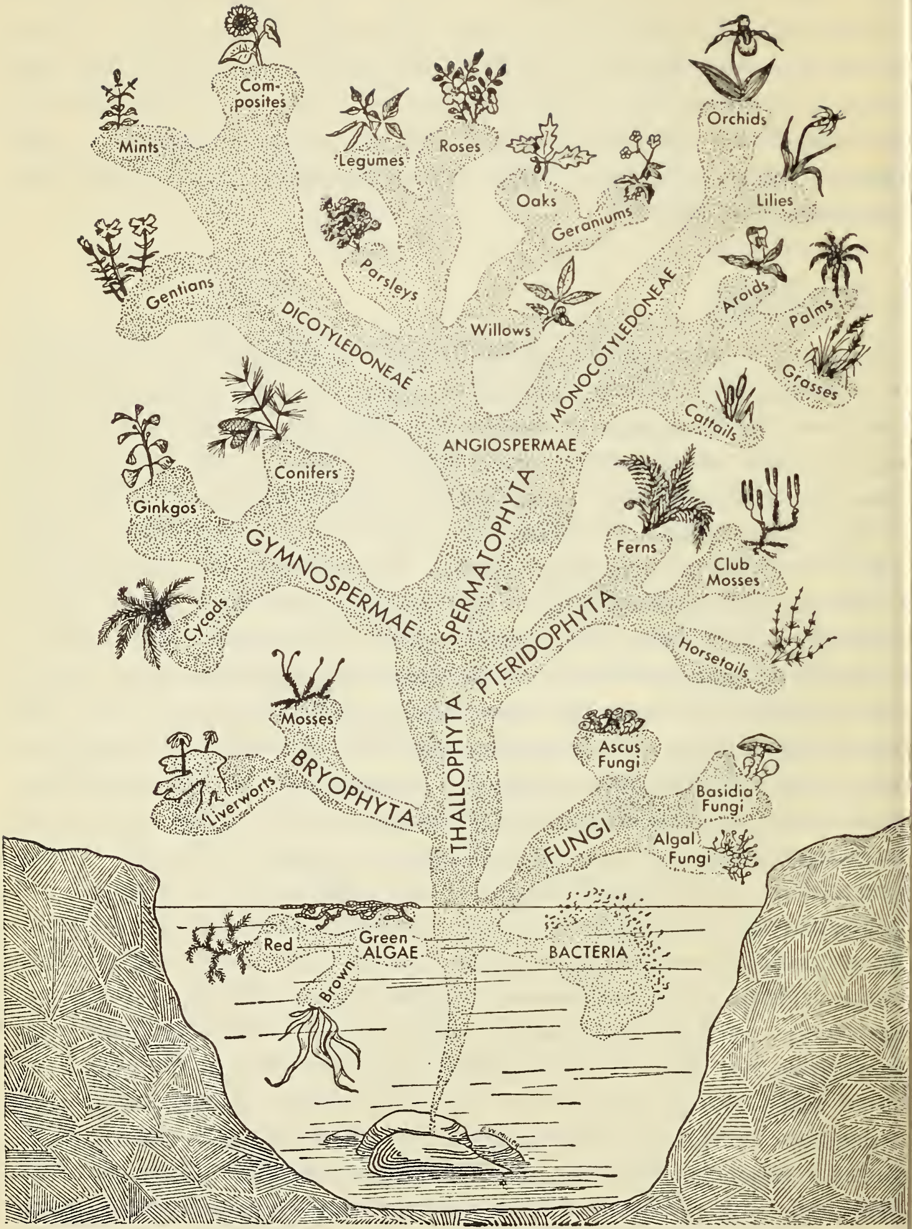

Fig. 3:1 Diagrammatic representation of evolution in plants.

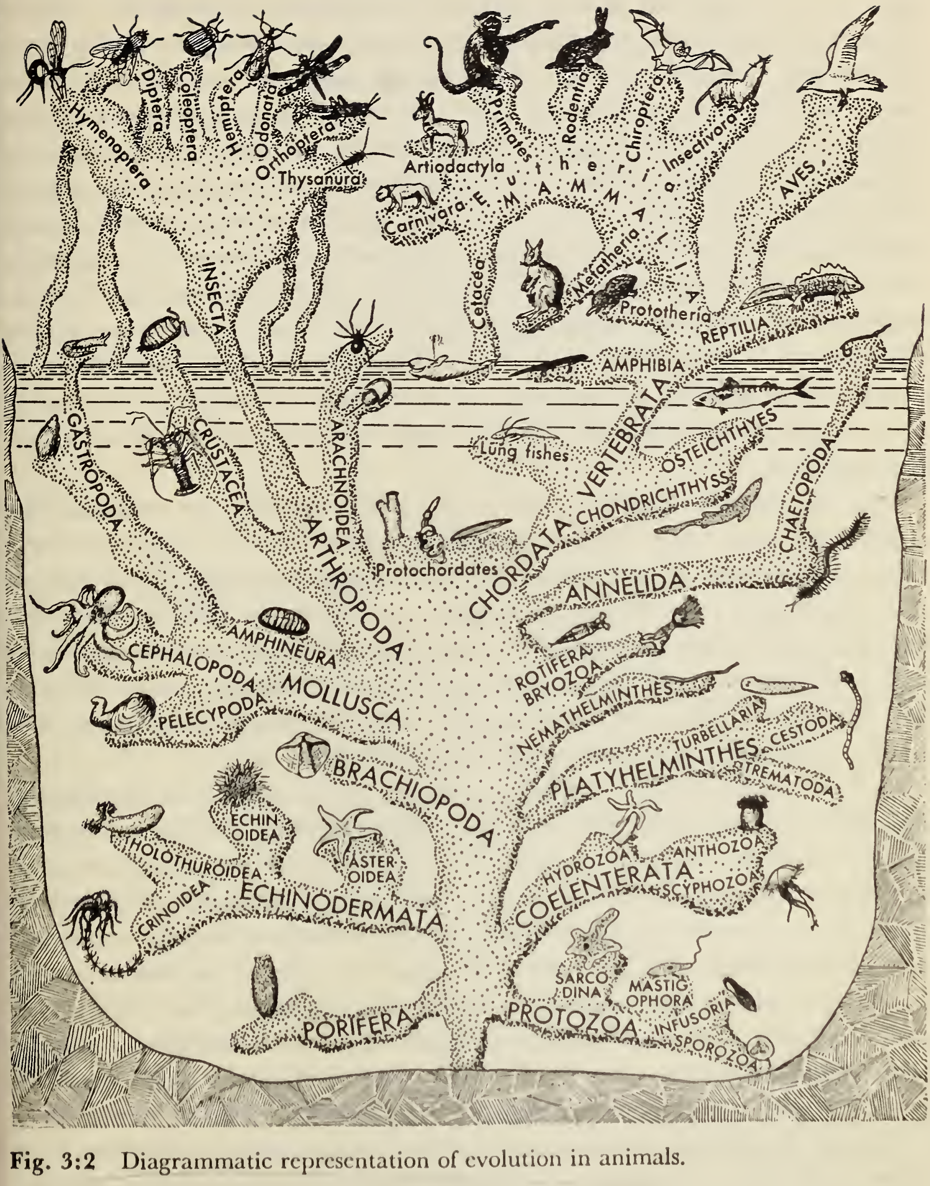

Fig. 3:2 Diagrammatic representation of evolution in animals.

here concerned particularly with organic evolution or the evolution of living things. This can be illustrated by a tree — a tree of life. The stem where it leaves the ground represents the most primitive organisms, or the origin of life in the distant past, perhaps a thousand million years ago. As the stem leaves the ground it divides into branches. These branches represent the origin of new and more complex forms from earlier and simpler forms. As time goes on and the tree ascends, these early branches in turn divide, and the early forms give rise to other slightly more highly organized forms, and so on until the ends of the branches are reached. Thus the tips of the branches represent the species living at the present time, and the older branches represent species which existed on the earth in earlier times from which those now in existence were descended and so show us the relationships between the species. Probably the first organisms were plants, since they must have manufactured their own food. Whether animals descended from plants or arose independently is doubtful. It is simplest, however, to compare the two great kingdoms of living things to two separate trees (Figs. 3:1 and 3:2).

The tips of the branches, that is the living species, are available for study and from their similarities and differences much regarding their relationships can be concluded, but the actual branches of the tree of life which show the real relationships are buried in the past and only rarely come to view as fossils. It should be noted that no living species can really be regarded as the ancestor of another living species. All that we can say is that they had a common ancestor which may or may not have resembled one of them more than the other.

Just as an individual is born, grows up, becomes mature, declines in old age, and eventually dies, so whole groups of plants and animals have arisen, evolved, become numerous, declined, and eventually become extinct. A conspicuous case of this was that of the great dinosaurs which lived in the age of reptiles. Just what caused them to become extinct is not entirely clear, but one attractive theory is that they became very highly specialized and adapted to particular environmental conditions, and that when these conditions changed they were unable to change with them. While the general trend of evolution seems to be ever onward to more highly developed and more perfectly adapted forms, there are many species and whole groups of plants and animals which seem to show regression, not, however, along the path of their earlier evolution, but rather along some side track entailing the loss or degeneration of organs or parts previously developed. An example of this is seen in animals, such as the blind fishes and blind salamanders found in caves.

It is known that the ancestors of these animals had well-developed eyes. When the species took to cave life their eyes gradually degenerated.

The scientific basis for constructing a tree of life will be considered later in this text. For the present it may be said that it is found in the results of careful studies of the anatomy and embryology of typical plants and animals, and the study of fossils. Such studies show, as previously indicated, that there are approximately twelve fundamental structural types (phyla) among animals and four, or perhaps more, fundamental structural types among plants. Differences in details of structure between the individuals of each fundamental type make it possible to recognize subtypes, and by going further and further into differences in detail to recognize smaller and smaller groups of animals and plants. In general, the greater the difference between two members of the same fundamental type, the earlier in the process of evolution must these differences have arisen. Thus in the vertebrate phylum the differences which led to the separation and evolution of birds and mammals must have appeared earlier than the differences which led to the separation and evolution of the gnawing mammals and the flesh-eating mammals.

3. THE ORIGIN OF LIFE

While the principle of organic evolution accounts for the great variety of plant and animal life, it makes no pretense at explaining the origin of life — how the first living things came into existence. The practically continuous occurrence of fossils in rocks of all ages, down to very early sedimentary rocks, shows that life began on the earth's surface relatively early in its history. Nevertheless the evidence from geology and astronomy shows that there probably was an earlier period during which life could not have existed on the earth's surface on account of its high temperature and the nature of its atmosphere. It therefore seems clear that life must either have come to our earth from some other part of the universe or have arisen *de novo* upon its surface.

We have no evidence of the actual transport of any form of living matter to our earth from elsewhere in the universe. Two ways have been thought of by which, conceivably, organisms might be transported to the earth: in the interior of meteors and as extremely minute forms propelled by the pressure of light. Any organism taking this journey would have to survive exceedingly low temperatures for an almost indefinitely long time. The spores of certain bacteria can survive a temperature approaching that below which no chemical reactions are known to take place, and the spores of others can endure a temperature as high as 120° C for a short time. At ordinary temperatures the seeds of some plants have been found to retain their vitality for nearly a hundred years. Whether any, even the simplest, organism could endure the greater hardships of a journey through interstellar space is doubtful. In any case, this theory, rather than providing a solution of the problem of the origin of life, merely serves to remove it to a part of the universe about which we know little or nothing and to place it beyond the possibility of solution.

If life began spontaneously on the surface of the earth, it is certain that the first organisms must have been extremely simple, more simple than any with which we are familiar. We have no evidence of how such simple organisms may have come into being, or of how simple inorganic substances may have combined together to form the first chemical compounds capable of absorbing and transforming energy, or how such chemical compounds may have been united to give the complex structure of protoplasm.

4. THE CLASSIFICATION OF ORGANISMS

The naming and classifying of organisms forms a special branch of biology called **taxonomy** or **systematics.**[1] Taxonomy includes, besides the actual naming of animals and plants and their arrangement in groups, the discussion of the rules applied in doing this and the natural laws which may be brought to light in the process.

Until the eighteenth century the different kinds of animals and plants were designated by their common or local names. For the purposes of exact and detailed studies such names are not satisfactory since: (*a*) the same organism frequently receives different names in different localities; (*b*) the same name is sometimes applied to different organisms; and (*c*) for many organisms — and here are included most microscopic animals and plants and most rare species — there are no common names. Taxonomists now use the **binomial system of nomenclature** in naming organisms. This system was introduced by the Swedish botanist, Linnaeus (1707–1778). Each different kind of organism is said to belong to a particular species (the word is the same in the singular and plural and the final "s" is pronounced) and like species are grouped into genera (singular, genus). The name of any particular animal or plant is then formed from the generic and specific names by placing the generic name first and following this with the specific name. The generic name is capitalized while the specific name, except in certain special cases, is usually not capitalized. Thus according to this system the name of the domestic dog is *Canis familiaris*, *Canis* (L. dog) being the name of the genus and *familiaris* (L. domestic) being the name of the species; and the name of the white oak is *Quercus alba*, *Quercus* (L. oak) being the generic name and *alba* (L. white) being the specific name.

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[1] "Taxonomy" (Gr. *taxis*, arrangement + *nomos*, law) is the more commonly used term in the United States, while "systematics" (L. *systema*, a placing together) is more commonly used in other English-speaking countries.

The famous Greek philosopher and scientist, Aristotle (384–322 B.C.), refers to about 500 different kinds of animals in his writings. In his *Systema Naturae*, the first edition of which was published in 1735, Linnaeus describes about 4000 species of animals. Recent estimates of the number of species of animals described to date place the number in excess of 800,000, or about two hundred times as many as were described by Linnaeus, and new species are continually being discovered. Not only are many more species known than in the time of Linnaeus but those which are known are in most cases much better known.

Fundamental to taxonomy is the idea conveyed by the term **species.** Linnaeus, like most of his predecessors and contemporaries, believed that species were fixed and unchanging and that therefore each species could be described precisely by listing a few "specific characters" which could be stated in precise terms and which were the same for all members of the species. This brief and precise method of describing species introduced by Linnaeus did much to advance taxonomy and to clarify the ideas of taxonomists. With some changes it continues to be the method in use at the present time. However, the concept of the term as expressed in the definition of a species has been modified to harmonize with the present knowledge of the geographical distribution, heredity, and life cycles of organisms. It is now known that species undergo slight but persistent changes and that the members of a species are by no means identical even in their specific characters. A species may be defined as a group of organisms which are similar morphologically and physiologically, which normally breed only within the group, and which have in common a certain complex of hereditary characters that in general constitute the characteristics of the species. Species are usually kept intact by some factor or factors, morphological, physiological, or geographical, which prevent them from interbreeding with the members of other species.

It is not enough simply to give the different species scientific names. The species must be classified or arranged according to some method. For a scientific study the classification should be such as to show the relationships between the different species. The relationships which modern classifications have aimed to show are those of descent or evolution. Species which show a close similarity of structure and external features and, therefore, are considered to have been descended from a previously existing species which did not differ greatly from either of them are placed in the same **genus**. Similarly, genera are grouped into **families**, families into **orders**, orders into **classes**, classes into **phyla**, and phyla into **kingdoms**. Of the latter there are two — the plant kingdom and the animal kingdom.

As an example let us take the domestic dog. We naturally place it in the animal kingdom. Within this kingdom are a dozen or more phyla, to one of which it must be assigned. It is placed among the chordates in the phylum Chordata. A satisfactory discussion of the reasons for this would lead us too far at the present stage of our study. Suffice it to say that the characters relate chiefly to structures which appear in the course of development and indicate certain fundamental features of structural plan. Because the dog possesses an internal skeleton including a backbone and skull and has many other special characteristics, it is placed among the vertebrates in the subphylum Vertebrata. Because it nourishes its young with milk from mammary glands and has many other characteristics including a covering of hair, it is placed among the mammals in the class Mammalia. Because its teeth and claws are adapted to the eating of flesh, it is placed among the flesh-eating mammals in the order Carnivora. This order contains a number of families, of which one is the family Canidae or dog-family, some of the distinguishing features of which are relatively straight legs for running, claws that cannot be retracted into the foot like those of a cat, a relatively long face, and numerous back teeth (molars). The family includes also the foxes. The name of the genus to which the domestic dog belongs is *Canis*, the Latin for dog. This is a large genus including also wolves and jackals. The species to which the dog belongs is *familiaris*.

Similarly in the case of the white oak, we recognize that it is a plant, and therefore place it in the kingdom Plantae. Since it bears seeds (the acorn is a fruit but it contains a seed), it is placed in the phylum Spermatophyta. Since it has flowers (they are very small but are true flowers), it is placed in subphylum Angiospermae. If we observe a seedling soon after it has emerged from the seed we see that it has two seed leaves and therefore place the plant in the class Dicotyledoneae. From a study of its flowers it would be put in the order Fagales which also contains the walnut, hickory, beech, and chestnut. A further study would enable us to put it in the family Fagaceae which includes the beech, chestnut, and oak. The leaves, acorns, and bark would indicate the genus *Quercus* (L. oak) and the species *alba* (L. white).

Kingdom	Animalia	Plantae
Phylum	Chordata	Spermatophyta
Subphylum	Vertebrata	Angiospermae
Class	Mammalia	Dicotyledoneae
Order	Carnivora	Fagales
Family	Canidae	Fagaceae
Genus	*Canis*	*Quercus*
Species	*familiaris*	*alba*

Thus the classification of plants and animals permits us to do three things: first, it makes it possible to give a definite and unequivocal name to each species; second, it enables us to place each species in a system which shows its relation to other species; and third, by arranging these species in classes, orders, and families, it makes possible a bird's-eye view of the whole world of living things. To obtain this bird's-eye view it is more important to know the main characteristics of the larger groups and to understand their relationships than to know the detailed classification of specific organisms, although examples are valuable for visualizing characteristics and relationships. The purpose of the following brief survey is to give the student a general view of the organic world.

5. PLANTS AND ANIMALS CONTRASTED

The roles which plants and animals play in the living world are dissimilar and in many respects complementary. Green plants manufacture organic food materials from inorganic materials in their environment. They are thus concerned with building up a store of energy in the form of chemical combination. Animals, on the other hand, are dependent upon green plants for their organic food materials. They utilize the energy which the green plants have stored.

The lowest plants and animals present many resemblances. Indeed there are numerous organisms which are claimed by both botanists and zoologists. However, very soon in the course of evolution the boundaries of the two great kingdoms of the organic world became established, and in their evolution there seems never to have appeared any real tendency for them to overlap. In Table 3:1 the main differences between plants and animals are summarized.

TABLE 3:1. PLANTS AND ANIMALS CONTRASTED

	PLANTS	ANIMALS
Food relations	Green plants manufacture their own organic food materials from inorganic materials obtained from the atmosphere, water, and soil. Nongreen plants are dependent on green plants but do not take solid food materials into their bodies	Animals are dependent on green plants for their organic food materials either directly by eating them or indirectly by eating nongreen plants or other animals
Energy relations	Plants, in general, because of their mode of life, are mainly concerned with storing up energy in the form of organic food materials	Animals, because of their active mode of life, are constantly using up the energy which they obtain ultimately from green plants
Activities	Most plants are either stationary or floating and not capable of locomotion. They usually react relatively slowly to stimuli	Most animals are capable of locomotion or, if fixed, of relatively rapid movement of some part of their bodies. They usually react quickly to stimuli
Cellular structure	Outside the plasma membrane plant cells are usually surrounded by cell walls composed of cellulose. It is these cell walls which give plants their rigidity	Animal cells while also surrounded by a plasma membrane are usually without rigid cell walls although they may secrete intercellular substances which become hard and rigid. Lack of rigid cell walls makes possible the movements of animals
Organization	The plant kingdom shows less variety of structure than the animal kingdom and the higher plants are less highly organized than the higher animals	The animal kingdom shows a greater variety of structure than the plant kingdom and the higher animals are more highly organized than the higher plants
Evolution	Apparently plants were unable to evolve beyond their first great phylum (thallus plants or Thallophyta) in the sea. The higher plants (mosses, ferns, and seed plants) have evolved on land, chiefly in response to the greater amount of light and free carbon dioxide available there and to the lack of water	The greater part of animal evolution to date has occurred in the sea where all the phyla are represented. Animals moved onto the land rather late in their evolution and few really fundamental changes have occurred in their structure since

6. A BRIEF SURVEY OF THE PLANT KINGDOM [1]

The plant kingdom is divided into four phyla[2] depending on the complexity of structure and the life history of the plants. Complexity of the plant body is due to the differentiation of cells to form different tissues and the differentiation of the body as a whole into parts or organs specialized to perform special functions. The number of species in the different groups gives an indication of their relative abundance since where there are numerous species there are usually numerous individuals, although this is not always the case: naturally when the individuals are large a given region supports a smaller number.

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[1] A more detailed classification is given in the Appendix.

[2] The term division is sometimes used by botanists in place of the term phylum as used here.

I. THALLUS PLANTS (Phylum Thallophyta)

About 80,000 species. The body of these plants consists of a thallus. A thallus may consist of a single cell or an aggregate of cells showing comparatively little differentiation into tissues; it is without true roots, stem, or leaves. The thallophytes constitute the lowest phylum of the plant kingdom.

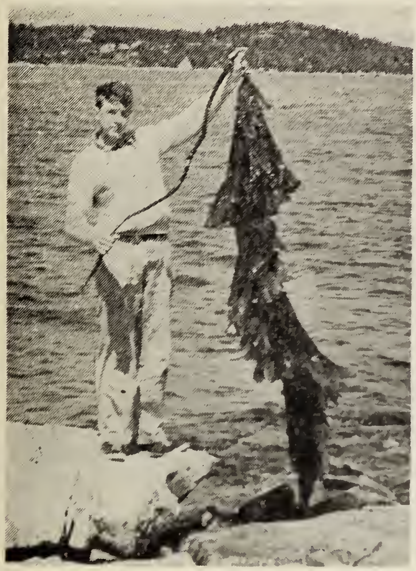

Fig. 3:3 A large marine alga, kelp (Laminaria, phylum Thallophyta, subphylum Algae). The boy grasps the holdfast by which the great ribbonlike thallus is attached to the ocean floor. Photograph by J. W. Mavor.

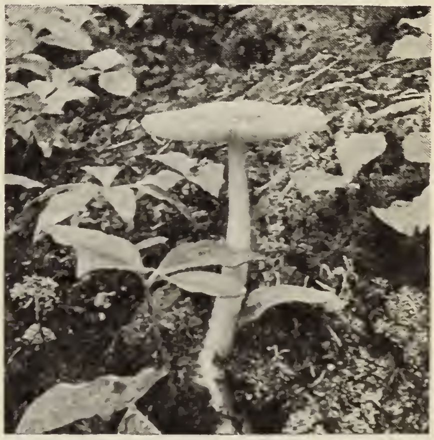

Fig. 3:4 A mushroom (phylum Thallophyta, subphylum Fungi), growing in a forest on decayed leaves and roots. Photograph by J. W. Mavor.

A. ALGAE (Subphylum Algae)

About 14,000 known species. Thallus plants with chlorophyll. Nearly all of these plants live in fresh or salt water, the greatest number being found in the sea. Fresh-water forms include the minute blue-green algae which sometimes form a slimy mass in stagnant ditches and dark films on moist ground (*Oscillatoria*, *Anabaena*, *Nostoc*); the pond scums (*Spirogyra*, *Zygnema*, and other genera), threadlike algae found floating in tangled masses near the surface of ponds; desmids, microscopic unicellular algae which take on quaint shapes; and the branched candelabra plants which grow up on the bottoms of ponds (*Chara*, *Nitella*). Marine forms include the sea lettuce (*Ulva*), rockweed (*Fucus*), and kelp (*Laminaria*) (Fig. 3:3).

B. FUNGI (Subphylum Fungi)

About 70,000 known species. Thallus plants without chlorophyll which, except in the case of certain bacteria, are dependent upon other plants or animals for their organic food stuffs. They include the bacteria; the different kinds of mold which attack bread, preserves, and fruits; mildews which attack the leaves and other parts of seed plants; the yeasts which cause fermentation; and mushrooms and toadstools (Fig. 3:4).

C. LICHENS

The lichens cannot be classified as a group of plants. Although a lichen has the appearance of a plant individual it is in fact composed of two plants, an alga and a fungus living together to their mutual advantage (Figs. 8:18 and 8:19). Lichens provide an excellent example of symbiosis, a condition in which two organisms of different species live together to the advantage of both.

II. THE LIVERWORTS AND MOSSES (Phylum Bryophyta)

About 20,000 known species. Mosses are small leafy plants common on moist ground but also found growing over rocks and fallen logs (Fig. 3:5). Liverworts are less familiar. One kind, known as the leafy liverworts, somewhat resemble mosses but differ from them in certain stages of their life cycle. The other kind of liverworts, in the stage of their life cycle most commonly seen, resemble a mass of small green leaves lying on the ground.

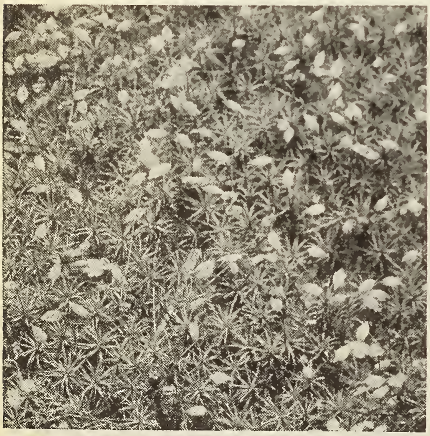

Fig. 3:5 A moss (*Polytrichum*, phylum Bryophyta) showing the gametophyte or leafy stage and the sporophyte stage with white spore capsules. Photograph by L. W. Brownell.

With the development of the mosses and the liverworts a great step toward the evolution of the seed plants was taken. This involves the alternation of a generation which reproduces sexually, known as the gametophyte, with a generation which reproduces asexually by means of spores, known as the sporophyte. In the mosses the gametophyte is represented by the leafy plant we all know, while the sporophyte is represented by a small capsule on the end of a long stalk extending from the tip of the gametophyte and appears frequently at certain periods of the year. The production of spores in the capsules makes possible the wide distribution of the plant on land by wind. In liverworts the spore-forming generation is simpler than in the mosses. In both liverworts and mosses the gametophyte is the conspicuous generation.

III. THE FERNS AND THEIR RELATIVES (Phylum Pteridophyta)

About 10,000 known species. Most of our common ferns have large, much divided leaves or fronds which grow up from an underground stem. The familiar fern plant produces spores and therefore belongs to the sporophyte generation. The spores are very minute but the capsules, or sporangia, in which they are formed can often be seen in little brown patches on the undersides of the leaves. When one of these spores reaches moist earth it grows into a minute plant which looks not unlike a small green leaf lying flat on the ground. This latter plant reproduces sexually and is called a gametophyte. From the fertilized egg a new sporophyte similar to the original fern plant develops. In the ferns the sporophyte is the conspicuous generation. By developing a more highly differentiated and independent sporophyte the ferns have made a step in advance of the mosses and liverworts toward the evolution of the seed plants (Fig. 3:6).

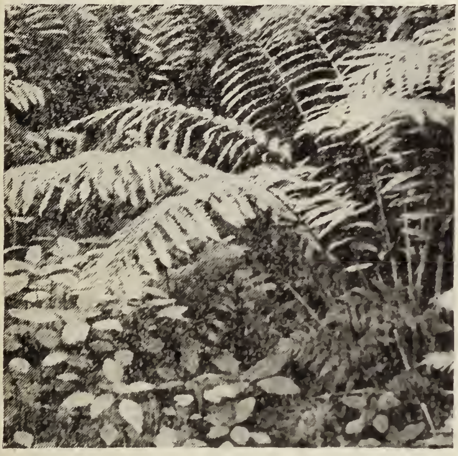

Fig. 3:6 Ferns (phylum Pteridophyta) growing by a small stream in the woods. Photograph by J. W. Mavor.

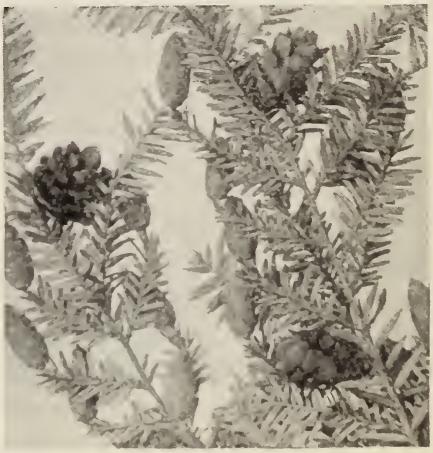

Fig. 3:7 Hemlock (*Tsuga*, phylum Spermatophyta, class Gymnospermae), an example of a conifer. The branch bears carpellate cones of two successive years. In the older ones the seed-bearing scales have separated. Photograph by L. W. Brownell.

IV. THE SEED PLANTS (Phylum Spermatophyta)

About 100,000 known species. Seed plants constitute by far the greater part of the vegetation of the earth. They include all trees, shrubs, and herbs and are the most highly evolved of the four phyla. The seed is the solution which these plants have arrived at for reproduction on land. A seed contains an embryo plant, provided with nourishment to begin its development, and resistant coats to protect it while awaiting the conditions necessary for this development. Trees, shrubs, or herbs are in reality sporophytes.

A. CONIFERS AND THEIR RELATIVES (Class Gymnospermae)

This group includes most cone-bearing plants. Most of them are either trees or shrubs. The cones take the place of the flowers of flowering plants. The seeds formed on the scales of the cones are not enclosed as they are in flowering plants. Examples of conifers are pine, hemlock (Fig. 3:7), ginkgo, cycad.

B. FLOWERING PLANTS (Class Angiospermae)

The flowering plants are adapted to life on land. Flowers by their colors and perfume attract insects which carry pollen from flower to flower. This has in turn led in many cases to adaptation between particular species of flowers and particular species of insects (Fig. 14:19). The ovule which forms the seed is enclosed in an ovary. Furthermore, the ovary usually develops to form a fruit. Fruits are adapted to different methods of dispersion. Fleshy fruits are fed upon by many species of birds and mammals which in return distribute the seeds. Other fruits, like those of the dandelion, are adapted for wind distribution. These different adaptations to pollination and seed distribution account in large measure for the great variety of flowers and fruits found in nature. Flowering plants are divided into two classes. These classes are in turn divided into orders and the orders into families. In the practical work of classifying flowering plants botanists have found the family the most useful. Most systematic works and keys place emphasis on this group. Families are often named after a prominent genus, as the rose family or the lily family.

(1)"Dicots" (Subclass Dicotyledoneae)

The embryo in the seed has two seed-leaves or cotyledons. The plants can usually be recognized by their net-veined leaves and their flowers in which the parts (sepals, petals, stamens, and carpels) are usually not in threes or multiples of three. Common and important "dicot" families are the buttercup, mallow, geranium (Fig. 3:8), mustard, carnation, primrose, phlox, snapdragon, rose, cactus, maple, parsley, and aster families.

(2) "Monocots" (Subclass Monocotyledoneae)

The embryo in the seed has only one seed-leaf or cotyledon. The plants can, in most cases, be recognized by their leaves which are usually parallel veined and their flowers which usually have their parts (sepals, petals, stamens, and carpels) in threes or multiples of three. Common and important families of "monocots" are the lily, iris (Fig. 3:9), palm, orchid, and grass families.

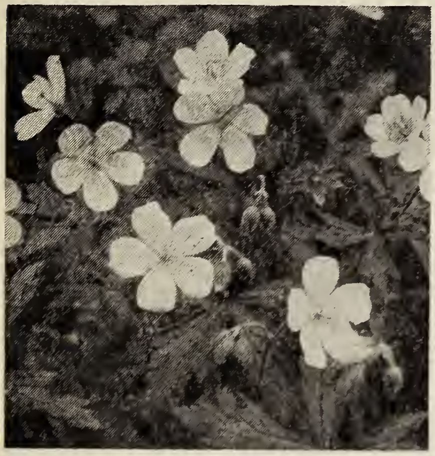

Fig. 3:8 A wild geranium (*Geranium*, phylum Spermatophyta, class Angiospermae, subclass Dicotyledoneae), an example of a "dicot." Note net-veined leaves and flowers with parts in fives. Photograph by L. W. Brownell.

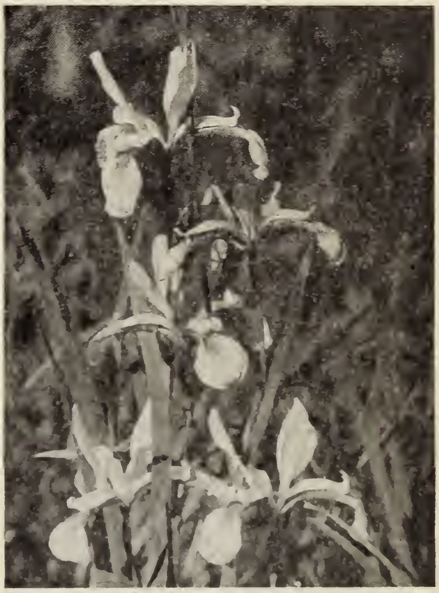

Fig. 3:9 The slender blue flag (*Iris*, phylum Spermatophyta, class Angiospermae, subclass Monocotyledoneae), an example of a "monocot." The leaves are parallel veined and the parts of the flowers are in threes.

7. A BRIEF SURVEY OF THE ANIMAL KINGDOM[1]

The differentiation between plants and animals must have occurred early in the evolution of organisms. Although there are some primitive unicellular forms which seem to be somewhat intermediate in structure and mode of life, these are few. The earliest animals, like the earliest plants, probably consisted of single cells or of masses of protoplasm not yet differentiated into cells. Multicellular animals may have developed when, after cell division, the daughter cells adhered to form groups in place of separating to lead independent lives. As in the case of plants, division of labor and structural differentiation followed — then tissues and organs. A much greater differentiation of the single cell is found in many of the unicellular animals than in any of the unicellular plants. Animal evolution has proceeded along many different paths represented by the many different phyla. The exact number of phyla differs in different schemes of classification, the difference being that in some classifications groups are regarded as separate phyla which according to other classifications are placed together in the same phylum. The following brief classification includes only those phyla which are relatively numerous and occur commonly.

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[1] A more detailed classification is given in the Appendix.

I. UNICELLULAR ANIMALS (Phylum Protozoa)

About 15,000 known species. Small animals consisting of a single cell or colonies of single cells. Locomotion when present is by means of irregular protoplasmic projections (pseudopodia), a few long whip-like extensions (flagella) or numerous fine hairlike structures which move in unison (cilia). These animals occur abundantly in both fresh and salt

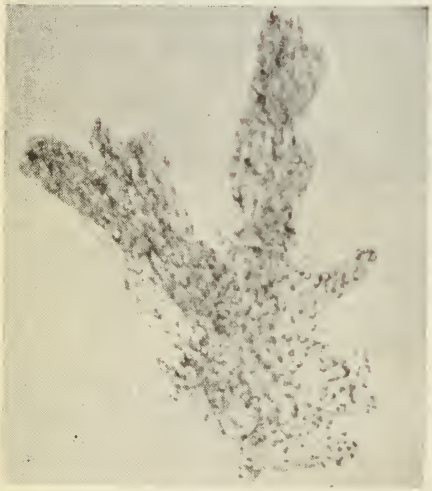

Fig. 3:10 Amoeba (phylum Protozoa). The animal is moving by means of two large pseudopodia towards the upper part of the field of the microscope. The outline of the single nucleus can be seen faintly near the center of the protoplasmic mass. Photomicrograph by J. W. Mavor.

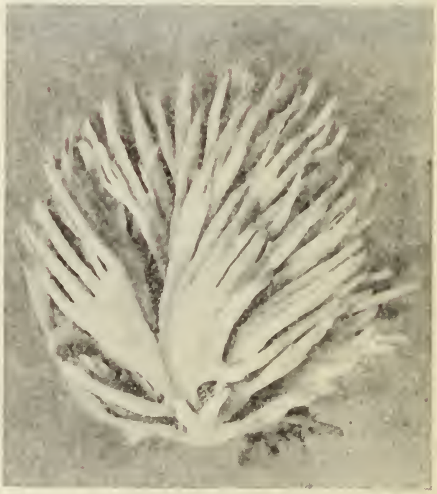

Fig. 3:11 A finger sponge (*Chalina*, phylum Porifera). A dried specimen on the sand of the seashore. Photograph by J. W. Mavor.

water and also as parasites in the bodies of other animals. *Amoeba* (Fig. 3:10), which has become famous as a biological type, is perhaps a relatively simple example of this phylum. In some cases, for example the slipper animalcule, *Paramecium*, the single cell may be quite complicated; in parasitic forms like the malaria parasite the life cycle may involve two hosts and several stages (Fig. 18:16).

II. SPONGES (Phylum Porifera)

About 3000 known species. Mostly marine. Irregularly shaped animals, usually attached to rocks or other objects in fresh or salt water (Fig. 3:11). There are numerous small openings on the surface of their bodies through which water enters and passes through a system of canals to be forced out again through one or more larger openings in the upper part of the animal. The common bath sponge consists of the dried skeleton of certain species of this group. Small fresh-water sponges are not uncommon in ponds.

III. POLYPS AND JELLYFISH (Phylum Coelenterata)

About 9500 known species. Aquatic animals which occur most frequently in the sea. Polyps are cylindrical animals which usually attach themselves by one end to some object in the water (Fig. 3:12). At the other end of the body is a ring of tentacles in the center of which is a mouth leading into a digestive cavity. The body wall surrounding this cavity and forming the tentacles consists of two layers of cells separated by a layer of jelly which is usually quite thin in the polyps. Characteristic of this phylum are the stinging cells, scattered over the surface of the body. When these cells are stimulated, fine threads are shot out and with them a poisonous substance fatal to many small, and irritating to many large, animals. A favorite polyp for biological study is the fresh-water *Hydra* described in Chap. 2. Other well-known examples are the

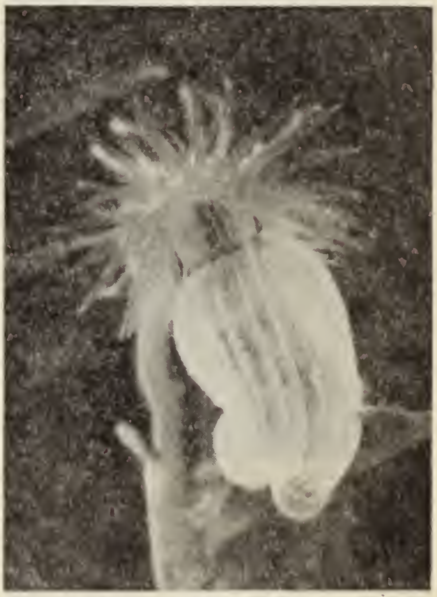

Fig. 3:12 A sea anemone (*Sagartia*, phylum Coelenterata). Note the tentacles which surround the mouth, which is not visible. The mesenteries are seen as longitudinal lines through the transparent outer body wall. Photograph by J. W. Mavor.

sea anemones (Fig. 3:12) and the corals. Coral polyps are attached forms. Where they are attached, usually to rocks, they form calcareous masses on which they become raised up. In this way they form reefs and islands. Many types of polyps form colonies, the younger individuals, which arise from the older by a process of budding or division, remaining attached. Jellyfish float in the water and are bell-shaped. Corresponding to what would be the clapper or tongue of the bell there is a tubular extension, on the end of which is the mouth. The digestive cavity takes the form of a series of canals connecting with a central portion. Most of the volume of the animal is made up of the jelly (Fig. 19:5).

IV. FLATWORMS (Phylum Platyhelminthes)

About 6000 known species. There are many kinds of "worms" and the flatworms are only one kind. Their bodies are elongated and flattened in a dorso-ventral or up-and-down direction and one end is differentiated into a head (Fig. 3:13). This makes them bilaterally symmetrical. There

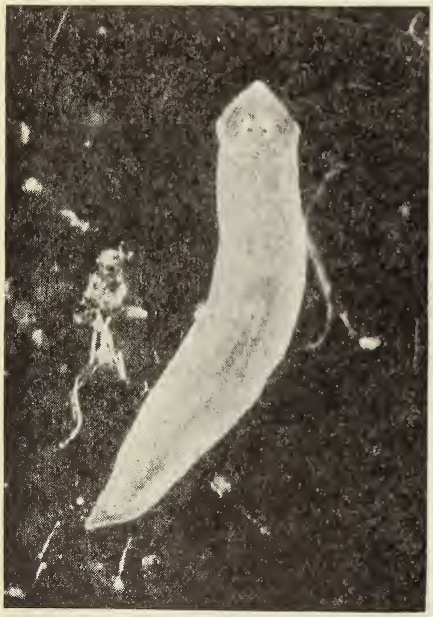

Fig. 3:13 A common fresh-water planarian (*Planaria*, phylum Platyhelminthes, class Turbellaria). The animal is moving toward the upper part of the field of the microscope. The two small dark bodies in the light areas are primitive eyes. Photomicrograph by J. W. Mavor.

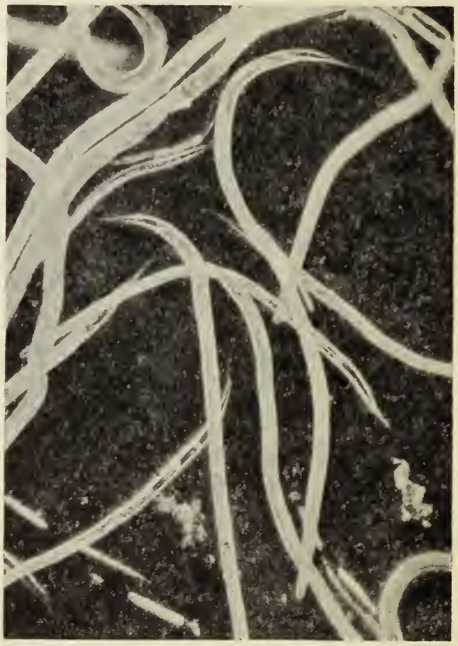

Fig. 3:14 Vinegar eels (*Turbatrix*, phylum Nemathelminthes) from a drop of vinegar. Photograph reproduced by permission of General Biological Supply House, Inc.

are three classes of flatworms which differ both in structure and in mode of life.

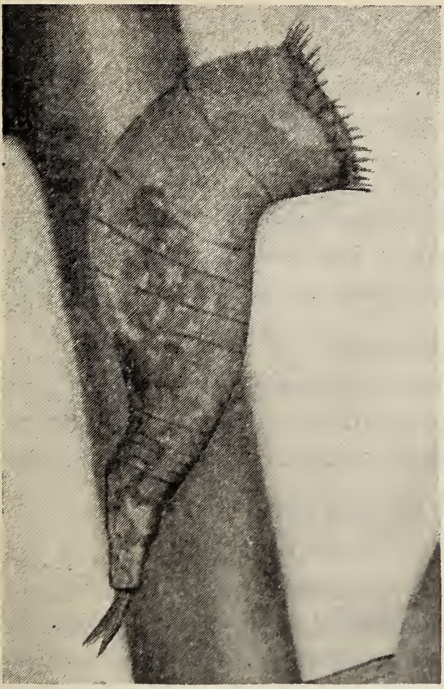

Fig. 3:15 A wheel animalcule of rotifer (*Cyrtonia*, phylum Rotifera). The circle of cilia is at the upper right side in the figure. Photograph of a model, reproduced by courtesy of the American Museum of Natural History, New York.

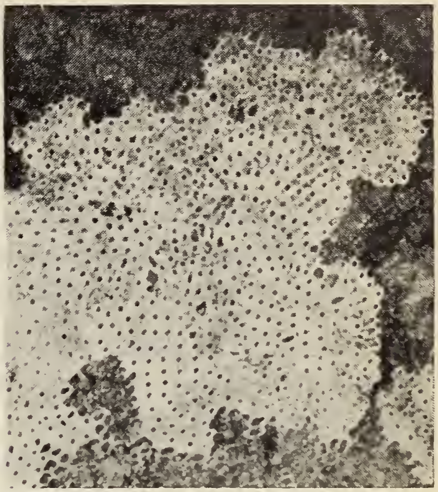

Fig. 3:16 A moss animal (*Microsporella*, phylum Bryozoa) incrusted on a rock. The black dots are the "cells" in which the animals live. Photograph by J. W. Mavor.

A. *PLANARIANS* (Class Turbellaria)

Free-living flatworms which glide through the water by means of cilia distributed over the surface of the body. They occur both in fresh water and in the sea. Most of them are small, under an inch in length (Fig. 3:13).

B. *FLUKES* (Class Trematoda)

Parasitic flatworms with suckers on the ventral surface, a mouth, and a digestive cavity. A well-known species lives in the liver of the sheep (Fig. 20:6).

C. *TAPEWORMS* (Class Cestoda)

Parasitic flatworms with no mouth or alimentary tract. The apparent segments or proglottids are in reality individuals budded off from the head end. They usually occur as parasites in vertebrates (Fig. 20:8).

V. ROUNDWORMS (Phylum Nemathelminthes)

About 8000 known species. The body is elongated and not segmented. The internal structure shows bilateral symmetry. The mouth at the anterior end leads into a long, straight digestive tube which opens to the exterior at the posterior end. They occur free-living in fresh water, in the sea, and on land, and as parasites in many different kinds of plants and animals (Fig. 3:14).

VI. WHEEL ANIMALCULES OR ROTIFERS (Phylum Rotifera)

About 1000 known species. Microscopic, multicellular animals which move about by means of circular bands of cilia near the mouth (Fig. 3:15).

VII. MOSS ANIMALS (Phylum Bryozoa)

About 1200 known species. Small, fixed, aquatic animals which form colonies attached to rocks, or to other animals, or to plants. The individual animals are multicellular but microscopic in size (Fig. 3:16).

VIII. STARFISHES AND THEIR RELATIVES (Phylum Echinodermata)

About 5000 known species. Radially symmetrical animals with a skeleton composed of calcareous plates and spines. Locomotion is chiefly by means of peculiar minute structures, called tube feet, with sucking disks. They occur only in the sea where they are relatively abundant.

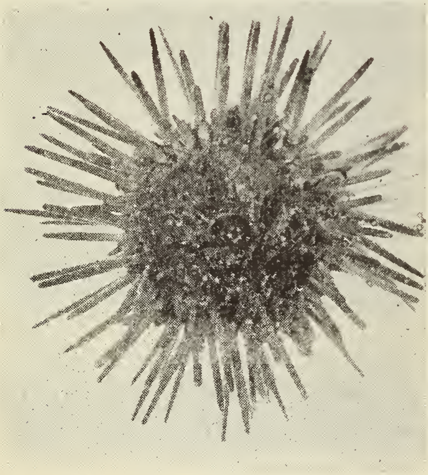

Fig. 3:17 A sea urchin (*Arbacia*, phylum Echinodermata). View of the under side showing in the center the five teeth surrounding the mouth and between the spines the suction disks of the tube feet. Photograph by J. W. Mavor.

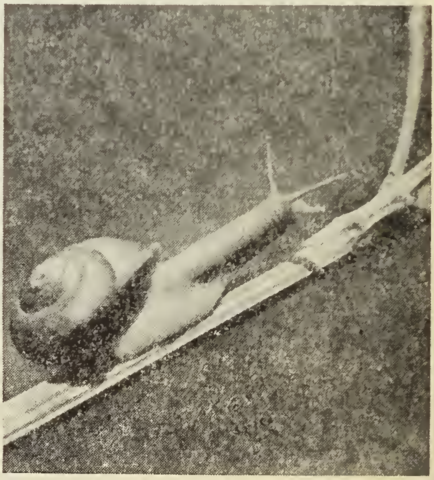

Fig. 3:18 A common land snail (*Polygyra*, phylum Mollusca, class Gastropoda). Photograph by L. W. Brownell.

Examples are starfishes, brittle stars, sea urchins (Fig. 3:17), sea cucumbers, and sea lilies.

IX. MOLLUSKS (Phylum Mollusca)

About 70,000 known species. Animals with soft inner bodies usually covered with a calcareous shell. There are five classes, the more frequently encountered of which are:

A. SNAILS AND SLUGS (Class Gastropoda)

Usually a single coiled shell (snails) (Fig. 3:18), sometimes no shell (slugs). They occur in the sea, fresh water, and on land. Examples: snails, slugs, periwinkles, whelk, oyster drill.

B. OCTOPUS, SQUID, AND THEIR RELATIVES (Class Cephalopoda)

Marine mollusks with large eyes and a well-developed head surrounded by long prehensile tentacles. Examples: squid (Fig. 39:56), octopus, devilfish, nautilus (with a coiled shell).

C. CLAMS, OYSTERS, AND THEIR RELATIVES (Class Pelecypoda)

Mollusks with a bivalved shell, i.e., one consisting of two lateral halves. They occur in fresh water and in the sea. Examples: clam (Fig. 39:50), oyster, mussel (Fig. 39:37), scallop (Fig. 39:53).

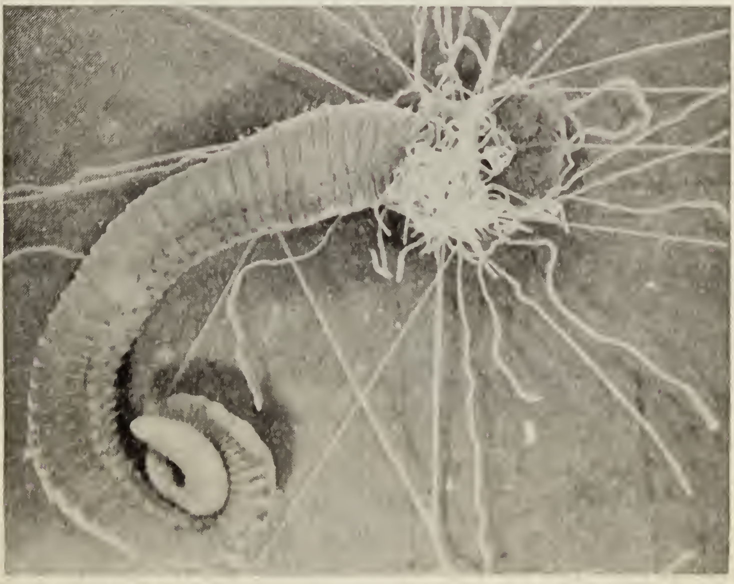

Fig. 3:19 A segmented bristle worm (*Amphitrite*, phylum Annelida). The head is toward the top of the picture. The white strands are tentacles which surround the mouth. Photograph by J. W. Mavor.

X. SEGMENTED WORMS (Phylum Annelida)

About 6500 known species. The body, which is wormlike and bilaterally symmetrical, is composed of a longitudinal series of ringlike segments. They occur in the sea, in fresh water, and on land. Examples: earthworm (Fig. 22:1), clamworm (Fig. 39:52), bristle worm (Fig. 3:19), leech.

XI. ARTHROPODS (Phylum Arthropoda)

About 640,000 known species. The name means "the jointed legged." The body, which is bilaterally symmetrical, is enclosed in a hard outer covering. This covering is jointed allowing movement. The body is segmented like that of an earthworm but the segments are usually combined to form a head, thorax, and abdomen. About half of all the species of living things are arthropods.

A. CRUSTACEANS (Class Crustacea)

Arthropods which breathe by means of gills and with a few exceptions spend their entire life in fresh water or the sea. Examples: water "fleas," fish "lice," barnacles (Fig. 39:36), crabs (Fig. 39:51), lobsters (Fig. 39:55), shrimps.

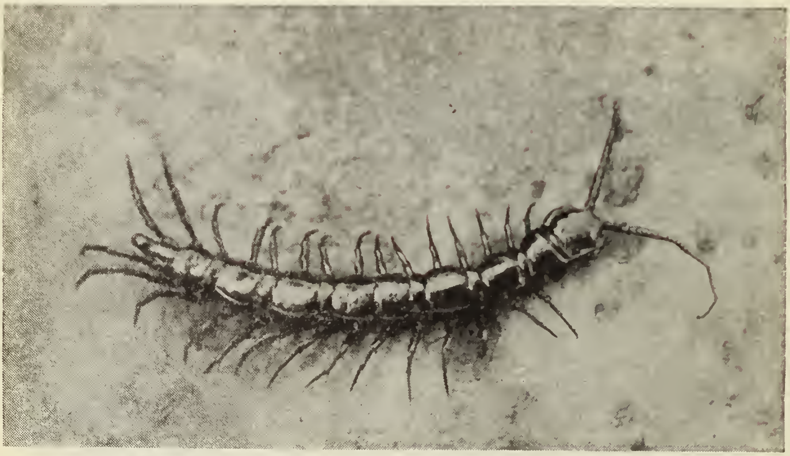

Fig. 3:20 A common centipede (*Lithobius*, phylum Arthropoda, class Chilopoda). Photograph by L. W. Brownell.

B. CENTIPEDES (Class Chilopoda)

Body flattened, segments except those of the head and tail similar and each bearing one pair of legs. They breathe air by means of air tubes (tracheae) and live on land (Fig. 3:20).

C. *MILLIPEDES* (Class Diplopoda)

Body cylindrical, apparent segments, except those of the head and tail, similar and each bearing two pairs of legs. They breathe air by means of air tubes (tracheae) and live on land.

D. *INSECTS* (Class Insecta)

Arthropods which breathe air by means of air tubes (tracheae). The body of the adult is usually divided into head, thorax, and abdomen. The head bears one pair of antennae. The thorax bears three pairs of legs and usually two pairs of wings (Fig. 3:21). The more highly developed groups of insects pass through a metamorphosis or change of form in their life cycle, the young animal or larva, often called a grub or worm, being quite different in its structure and mode of life from the adult. To effect the change from larva to adult the animal may go into a quiescent stage forming a pupa which is often enclosed in a cocoon. The characters most commonly used in classifying insects are type of metamorphosis, wings, and mouth parts. Some insects like the little bristletails or "fish moths" seen in cupboards and cellars go through their life cycles without a metamorphosis (ametabolic), the larva being similar to the adult. Other insects like the grasshoppers have a gradual or partial metamorphosis (hemimetabolic), changing gradually into adults without any resting or pupal stage, the young and immature stages being called nymphs. Still other insects like the butterflies have a complete metamorphosis (holometabolic), the larva forming a pupa or cocoon in which it undergoes an extensive reorganization into the

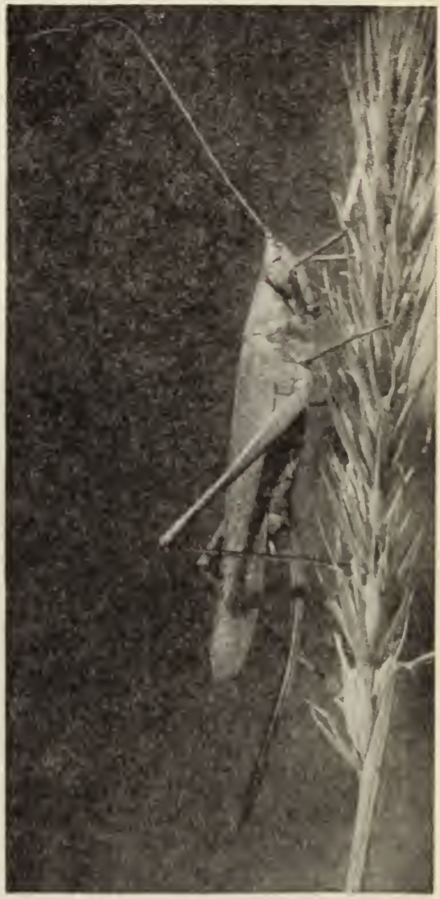

Fig. 3:21 A long-horned grasshopper or katydid (*Conocephalus*, phylum Arthropoda, class Insecta). Photograph by L. W. Brownell.

adult which is often very different from it not only in structure but in mode of life. Typically an insect has two pairs of wings. These, however, may be absent as in the bristletails or the worker caste of ants, or there may be only a single pair as in flies. Further, both pairs may be membranous (dragonflies), or the front pair may be parchmentlike (grasshoppers), or form a protective covering (beetles), or both pairs may be covered with scales (butterflies and moths). The mouth parts may be adapted for chewing, piercing, and sucking, for sucking only, or vestigial (i.e., reduced to such an extent as to be useless). There are more species of insects than of all other animals. Many different orders are distinguished. The following list includes the common names of representatives of some of the larger and better known of these orders (Fig. 24:9). (A more detailed classification is given in the Appendix.)

Bristletails
Springtails
Grasshoppers
Termites
Aphis lions
May flies
Dragonflies
Stone flies
Bird lice
Bugs
Plant lice
Earwigs
Beetles
Caddis flies
Moths and butterflies
Flies
Fleas
Bees, wasps, and ants

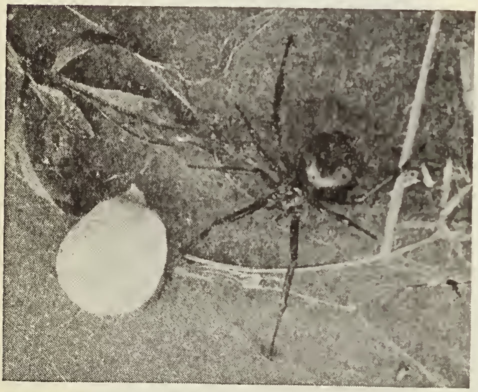

Fig. 3:22 Black widow spider (*Lathrodectus*, phylum Arthropoda, class Arachnoidea). Female with cocoon containing eggs. The cocoon shows as the large white body on the left. Photograph reproduced by courtesy of *Nature Magazine*, Washington, D. C.

E. SPIDERLIKE ANIMALS
(Class Arachnoidea)

Body usually divided into an anterior portion composed of head and thorax, to which the legs are attached, and a posterior portion consisting of a spherical abdomen. They have no antennae and no true jaws. Examples: scorpions, Limulus (Fig. 39:47), spiders (Fig. 3:22), daddy longlegs, mites, and ticks. Unlike insects, the spiders, daddy longlegs, mites, and ticks have four pairs of walking legs.

XII. CHORDATES (Phylum Chordata)

About 70,000 known species. With the exception of a few species which are regarded as connecting links with the lower phyla, the chordates are all vertebrates. We therefore proceed directly to this group.

VERTEBRATES (Subphylum Vertebrata). Animals which have a vertebral column or backbone composed of segments or vertebrae, which breathe by means of pharyngeal gills or lungs, which have their central nervous system on the upper or dorsal side of the body, and which have typically two pairs of appendages.

A. LAMPREYS (Class Cyclostomata)

Jawless, round-mouthed, eel-shaped fishes, with a cartilaginous skeleton and no lateral fins (Fig. 26:6).

B. SHARKS AND RAYS (Class Chondrichthyes)

Fishes with jaws, a cartilaginous skeleton and lateral fins, which breathe by means of platelike gills in gill chambers which open separately to the exterior except in the deep sea fishes known as chimeras. The body is covered with minute platelike scales imbedded in the skin with teethlike structures projecting through the epidermis (Fig. 26:7).

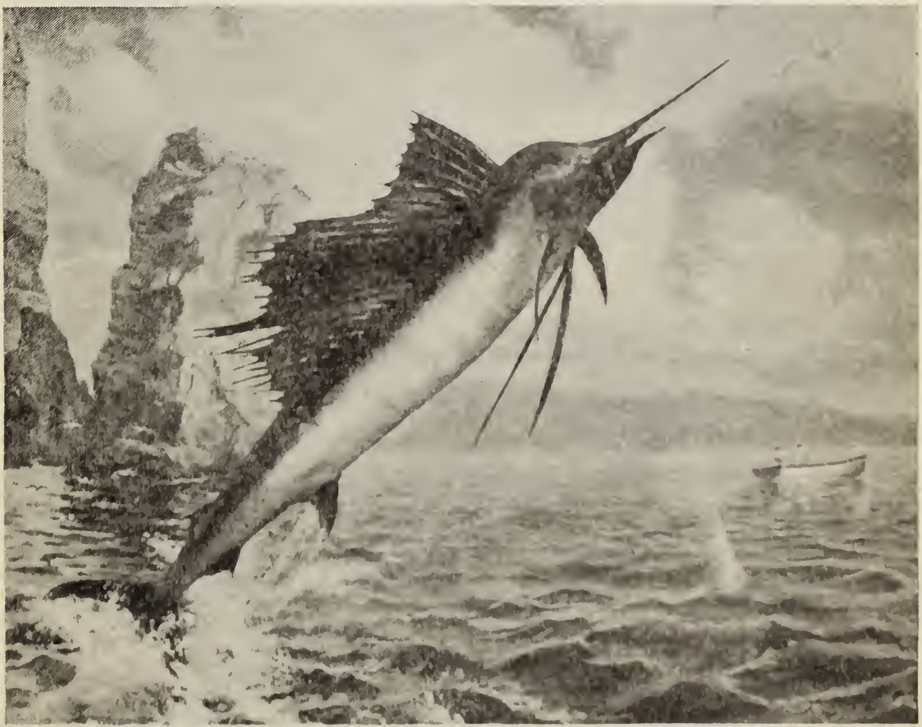

Fig. 3:23 A sailfish (*Istiophorus*, phylum Chordata, subphylum Vertebrata, class Osteichthyes) caught on a line. Photograph of a sketch by A. A. Jansson reproduced by courtesy of the American Museum of Natural History, New York.

C. BONY FISHES (Class Osteichthyes)

Fishes with jaws and lateral fins and a bony skeleton, which breathe by means of gills in a gill chamber which is covered by a bony flap known as an operculum and opens to the exterior on either side of the head. This class includes nearly all of the common fresh-water and marine fishes except the sharks and rays. There are a great many species and their variety is as great as that of the birds of the air. Of great interest, from the point of view of the evolution of the next class (Amphibia), are the now rare lungfishes, a special group of the bony fishes. Examples: perch, trout, swordfish, salmon, sailfish (Fig. 3:23).

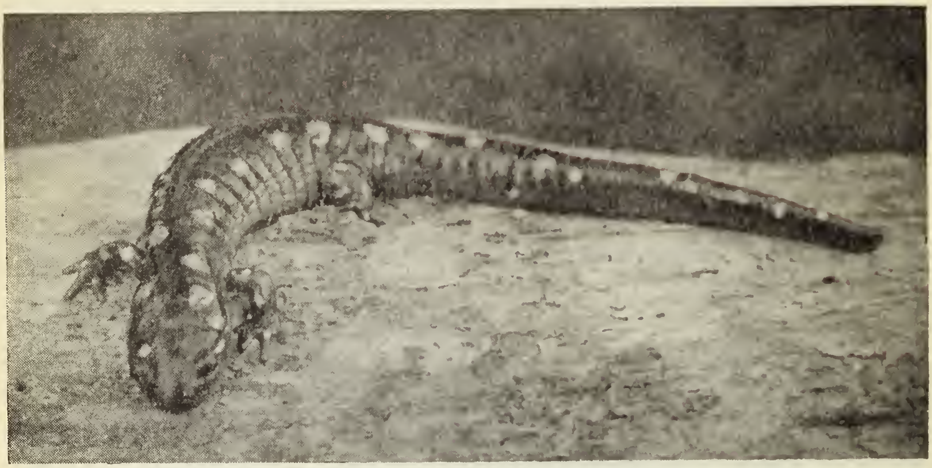

Fig. 3:24 A spotted salamander (*Ambystoma*, phylum Chordata, class Amphibia). Photograph by L. W. Brownell.

D. AMPHIBIANS (Class Amphibia)

The name has its origin in the fact that many species when young live in water and when older in air, e.g., frog. Breathing is by means of gills in the larval or tadpole stage and through the skin and lungs in the adult. In the adult stage there are two pairs of pentadactyl (i.e., five-toed) limbs without claws. The body is without scales except in certain tropical legless forms. Examples: frogs (Fig. 27:1), toads, salamanders (Fig. 3:24), newts.

E. REPTILES (Class Reptilia)

Reptiles breathe air throughout their lives. Their scales are horny and formed from the outer layer or epidermis of the skin. There are usually two pairs of appendages, snakes being a notable exception, which are usually pentadactyl (i.e., five-toed). Examples: turtles (Fig. 3:25), tortoises, lizards (Fig. 39:10), snakes (Fig. 39:30), crocodiles, and alligators.

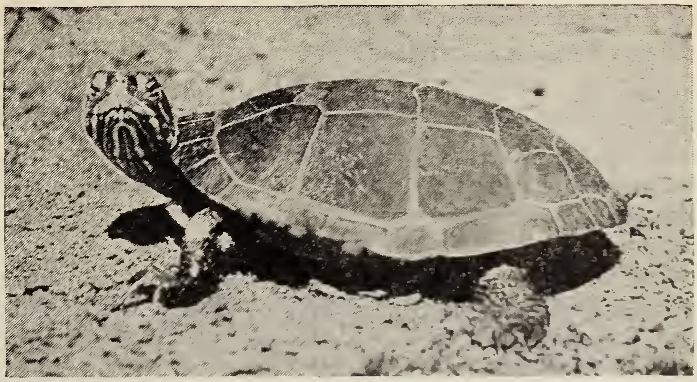

Fig. 3:25 A painted mud turtle (*Chrysemys*, phylum Chordata, class Reptilia). Photograph by J. W. Mavor.

F. BIRDS (Class Aves)

The body is covered with feathers and the fore limbs are modified to form wings (Fig. 3:26). No living birds have teeth, their place being taken by a horny beak. The common names of some of the more familiar orders of birds follow.

Flightless, terrestrial birds, usually of large size, without a keel on the breastbone (division Ratitae):

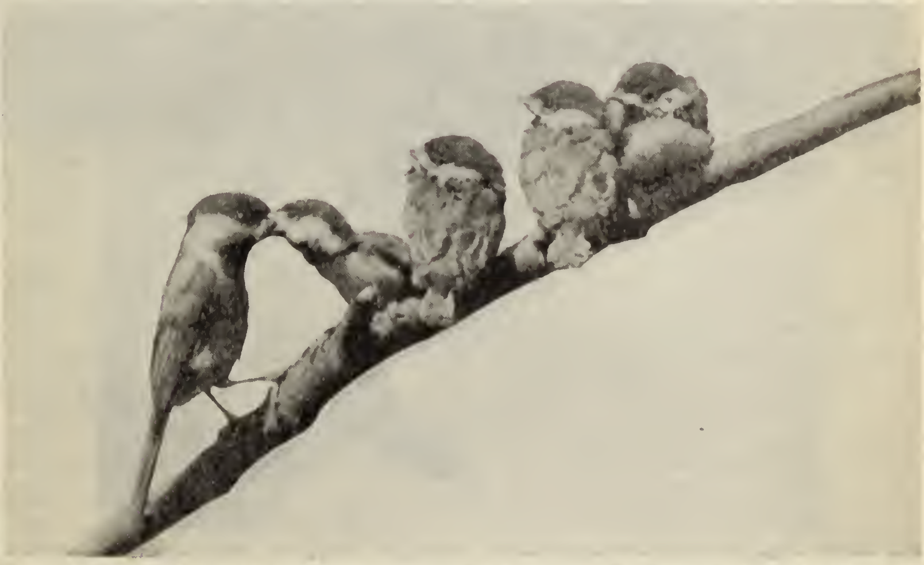

Fig. 3:26. A chickadee (*Penthestes*, phylum Chordata, subphylum Vertebrata, class Aves) feeding its young. Photograph by L. W. Brownell.

- Ostriches
- Rheas
- Emus
- Kiwis

Flying or diving birds with a keel on the breastbone, including nearly all living birds (division Carinatae):

- Penguins
- Loons
- Grebes
- Albatrosses and petrels
- Pelicans and cormorants
- Storks, herons, and flamingoes
- Geese and ducks
- Eagles, hawks, and vultures
- Fowls, pheasants, and turkeys
- Cranes
- Gulls and sandpipers
- Pigeons and doves
- Parrots
- Cuckoos
- Owls
- Goatsuckers
- Swifts and hummingbirds
- Kingfishers
- Woodpeckers
- Perching birds

The perching birds (order Passeriformes) include more than half of all the known species of birds. Examples are larks, swallows, crows, jays, chickadees (Fig. 3:26), wrens, thrushes, robins, starlings, blackbirds, and sparrows.

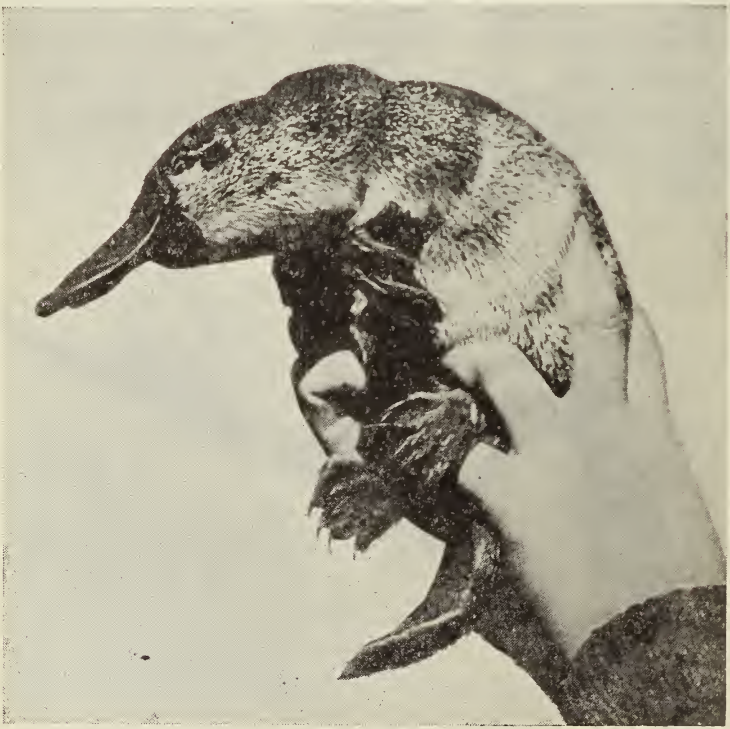

Fig. 3:27 The duckbill (*Ornithorhynchus*, phylum Chordata, subphylum Vertebrata, class Mammalia, subclass Prototheria), an egg-laying mammal. Photograph reproduced by permission of the Australian National Travel Association.

G. *MAMMALS* (Class Mammalia)

The name refers to the method of nourishing the young with milk from mammae or breast glands. Mammals are also distinguished by the possession of hair.

(1) Egg-laying mammals (Subclass Prototheria)

The most primitive of existing mammals, found only in Australia, Tasmania, and New Guinea. They live in burrows where their small leathery-shelled eggs are laid and their very immature young are raised and fed on a milky secretion from the mother. Examples: duckbill (Fig. 3:27) and echidna.

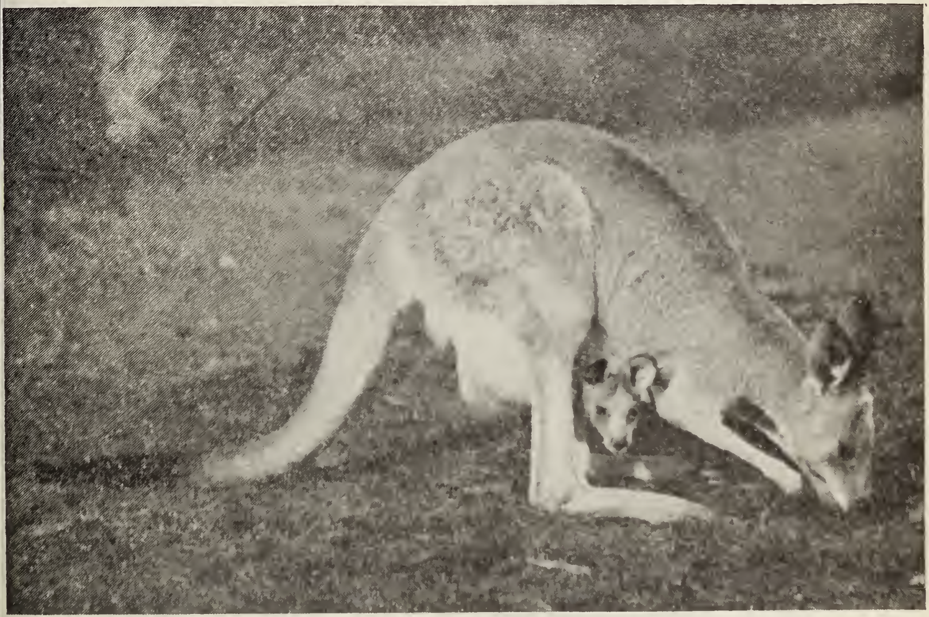

Fig. 3:28 A kangaroo (*Macropus*, phylum Chordata, subphylum Vertebrata, class Mammalia, subclass Metatheria) with a young one in its pouch. Photograph reproduced by permission of the Australian National Travel Association.

(2) Pouched mammals (Subclass Metatheria)

The young are born in a very immature condition and are carried in a pouch on the underside of the body of the mother. Examples: opossum, kangaroo (Fig. 3:28), koala.

(3) Placental mammals (Subclass Eutheria)

Mammals in which the mother retains the young in her body for a considerable time, nourishment being provided by her through a special organ known as the placenta (described in Chap. 35). This subclass includes most wild and domesticated mammals. Examples of the subclass include mole, bat, dog, wolf, skunk, cat, lion (Fig. 3:29), seal,

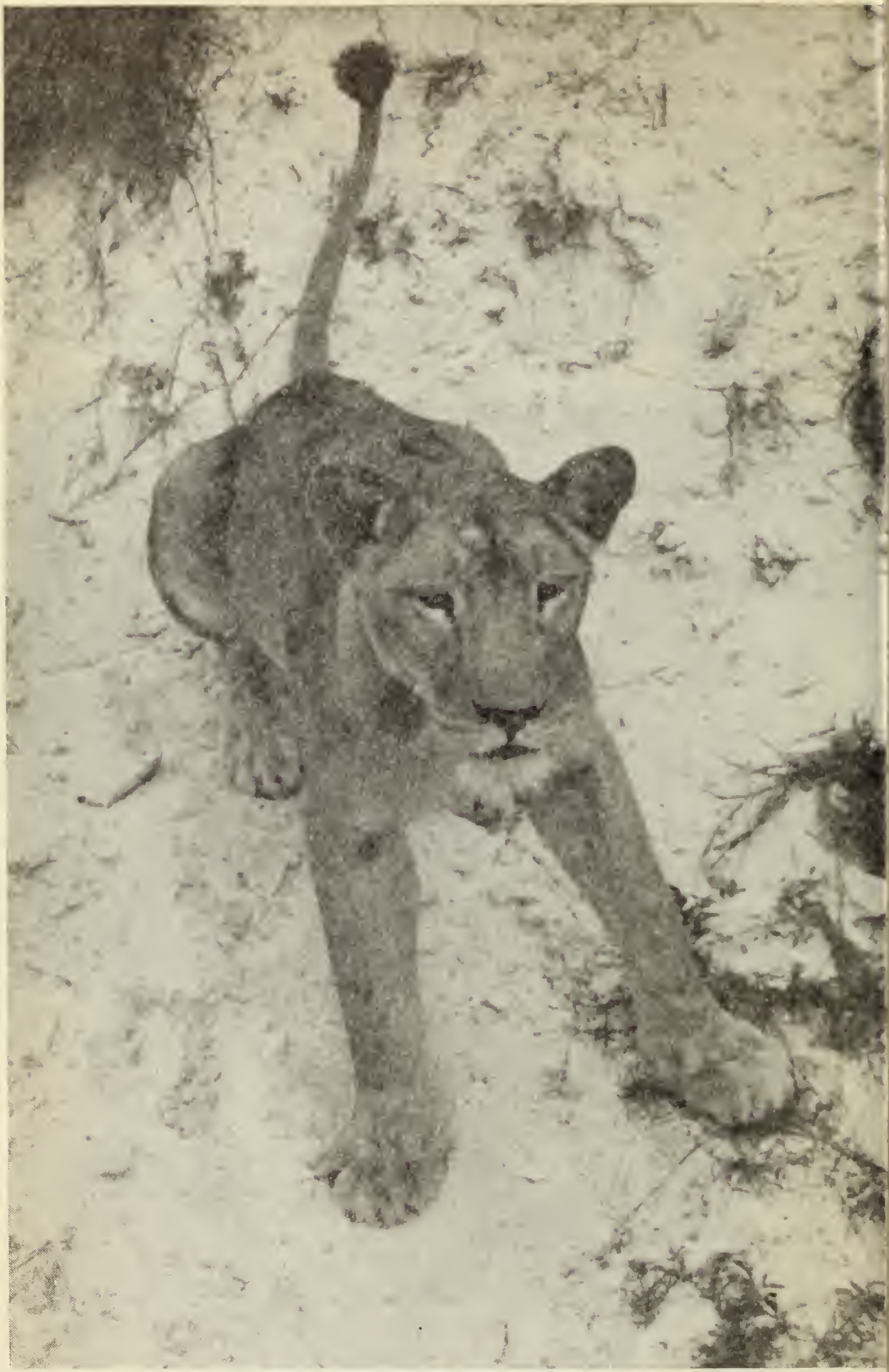

Fig. 3:29 A lion cub (*Leo*, phylum Chordata, subphylum Vertebrata, class Mammalia subclass Eutheria). Photograph on Agfa film reproduced by permission of the Agf Ansco Corporation.

walrus, monkey, ape, sloth, mouse, rat, squirrel, muskrat, beaver, porcupine, rabbit, deer, giraffe, camel, ox, horse, tapir, rhinoceros, elephant, whale, dolphin.

Topical Outline of Chapter 3

1. Structure and adaptation 52
2. Evolution 55
3. The origin of life 59
4. The classification of organisms 60
5. Plants and animals contrasted 63
6. A brief survey of the plant kingdom 64
7. A brief survey of the animal kingdom 69

Questions

1. Distinguish clearly between structure, function, and adaptation using several examples taken from both the plant and animal kingdoms.
2. Elaborate on the statement, "the act of living imposes certain restrictions on the structure of an organism," discussing examples such as the following: "Why are there no three-legged rabbits?" "elephants with wings?" "mice with horns?" " insects as large as elephants?" etc.
3. In which groups are the following classified and why: duckweed, palm tree, rockweed, whale, bat, snake, frog, eel, maggot, slug, scallop, sea cucumber, tapeworm, sea anemone, sponge?
4. State in your own words what you understand by the term "evolution."
5. Compare the naming of a species with the naming of a person.
6. What is the aim of a natural system of classification of plants and animals?
7. Walk through a forest and try to classify the plants and animals you see into the groups outlined in this chapter. For the present it is more important to recognize the main groups than to determine the exact species.
8. If a natural history museum is available, visit it to get a general idea of the main groups of plants and animals.

Suggestions for Further Reading[1]

Hylander, C. J., *The World of Plant Life*, The Macmillan Company, New York, 1939. A popular account of plants from the systematic point of view.

Pool, Raymond J., *Flowers and Flowering Plants, An Introduction to the Nature and Work of the Flowers and the Classification of Flowering Plants*, McGraw-Hill Book Company, Inc., New York, 1929.

Fassett, Norman C., *A Manual of Aquatic Plants*, McGraw-Hill Book Company,

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[1] In this and the following lists of suggestions for further reading the more general books are placed first and the books dealing with individual groups are listed in the order in which the groups are referred to in the chapter.

Inc., New York, 1940. An excellent book for determining and classifying aquatic plants.

Hegner, Robert W., *Parade of the Animal Kingdom*, The Macmillan Company, New York, 1937. An interesting and well-illustrated book describing many different types of animals.

Buchsbaum, Ralph, *Animals without Backbones*, University of Chicago Press, Chicago, 1938. A profusely illustrated and interestingly written account of the invertebrates.

Comstock, J. H., and A. B. Comstock, *A Manual for the Study of Insects*, Comstock Publishing Company, Inc., Ithaca, N. Y., 1936. A general account of insects.

Lutz, Frank E., *Field Book of Insects*, G. P. Putnam's Sons, New York, 1918. A useful book for determining the names of insects found in the field.

Jordan, David S., *Fishes*, American Nature Series, D. Appleton and Company, New York, 1907. A good book for the different species of fishes.

Kyle, H. M., *The Biology of Fishes*, The Macmillan Company, New York, 1926. A book on the life of fishes and the biological problems involved.

Barbour, Thomas, *Reptiles and Amphibians: Their Habits and Adaptations*, Houghton Mifflin Company, Boston, 1926.

Ditmars, Raymond L., *Reptiles of the World*, The Macmillan Company, New York, 1937. An interesting, well-illustrated book.

Allen, Arthur A., *The Book of Bird Life*, D. Van Nostrand Company, Inc., New York, 1930. A good book about birds but not a manual for determining names.

Hamilton, W. J., Jr., *American Mammals, Their Lives, Habits, and Economic Relations*, McGraw-Hill Book Company, Inc., New York, 1939. Descriptions of the lives of mammals and the conditions under which they live.

Driver, E. C., *Name That Animal*, published by the author, Northampton, Mass., 1942.

CHAPTER 4

The Cell

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1. THE CELL PRINCIPLE, ITS HISTORY AND SIGNIFICANCE

About 280 years ago, one of the early microscopists, an Englishman by the name of Robert Hooke, amused himself by looking at sundry small objects with his latest improvement of the then rather primitive compound microscope (Fig. 4:1). He recorded his observations in a book which he called *Micrographia*, literally, a writing about small things, which was published in 1665 and from which the following is quoted:

> I took a good clear piece of cork, and with a pen-knife sharpen'd as keen as a razor, I cut a piece of it off, and thereby left the surface of it exceeding smooth, then examining it very diligently with a microscope, me thought I could perceive it to appear a little porous; but I could not so plainly distinguish them, as to be sure that they were pores, much less what figure they were of: but judging from the lightness and the yielding quality of the cork, that certainly the texture could not be so curious, but that possibly, if I could use some further diligence, I might find it to be discernable with a microscope, I with the same sharp penknife, cut off from the former smooth surface an exceeding thin piece of it, and placing it on a black object plate, because it was itself a white body, and casting the light on it with a deep plano-convex glass, I could exceeding plainly perceive it to be all perforated and porous, much like a honey-comb, but that the pores of it were not regular; yet it was not unlike a honey-comb. . . ." (Fig. 4:2)

To the separate small compartments which he was able to see in the cork Robert Hooke gave the name "cells." We now know that cork consists of dead tissue from which the living material has disappeared. Not until much later (1835) was attention paid to the material inside the "cells" when Dujardin recognized this to be the actual living material. To this material von Mohl gave the name **protoplasm** (Gr. *protos*, first + *plasma*, form). The nucleus was apparently seen by Fontana in 1781, but the discovery of its general occurrence in cells is usually credited to Robert Brown in 1831. The significance of the nucleus was not appreciated until later when it was realized that it plays an important role in the life of the cell.[1]

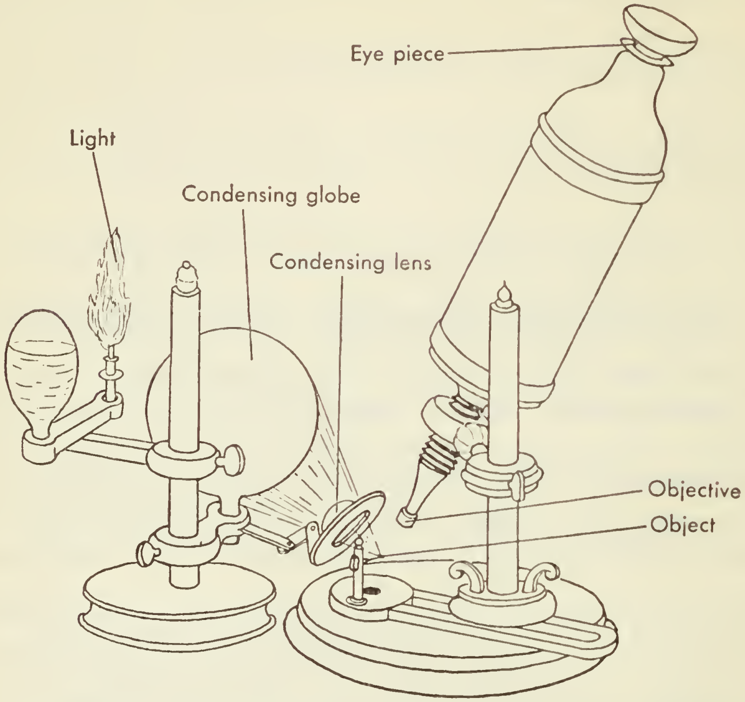

Fig. 4:1 Compound microscope used by Robert Hooke in the seventeenth century (about 1660). With this microscope Hooke discovered the cellular structure of cork. Redrawn after Carpenter, *The Microscope.*

The great importance of these discoveries regarding the cell was not recognized until after the enunciation of the **cell principle,** at first called the cell theory. The statement of this theory is generally attributed to two Germans, Jakob Schleiden and Theodor Schwann.[2] Schleiden announced the theory for plant tissues in 1838. Schwann announced the theory for animal tissues in the same year and later in 1839 developed the general theory and applied it to all living organisms. In his own words, "All organized bodies are composed of essentially similar parts, namely cells. . . . The whole organism subsists only by means of the reciprocal action of the single elementary parts." Today we would include also cell products. **Cell products** are substances formed by the cells which remain within them or are passed out through the plasma membrane in liquid form to later either remain as fluids, such as the blood and lymph, or to be coagulated into solid materials, such as the solid part of bone or the cell walls of plant cells. A statement of the cell principle would now run somewhat as follows: the unit of plant and animal organization is the cell, and all plants and animals are composed of cells and their products, a cell being defined as a nucleated mass of protoplasm capable of carrying on its own vital activities.

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[1] As outlined above, the word "cell" as a biological term was first used by Robert Hooke for the nonliving cases or compartments which form so prominent a feature of plant tissues. Much confusion would have been avoided and both the rules and the harmony of biological terminology would have been preserved if the term had retained this meaning. However, with the discovery of protoplasm and its significance as the actual living material, the connotation of the word cell was extended to include the "cell" contents. Then when the study of animal tissues showed that they also contained unit masses of protoplasm but without the cell walls so evident in plant cells, the naked protoplasm was called a cell. To correct the inconsistency the word protoplast has been introduced to designate the living protoplasmic unit as distinct from the nonliving cell walls, but cell still persists as the more generally used term.

[2] Historical research has shown that a Frenchman, Dutrochet, preceded Schleiden and Schwann in the development of the cell theory. Indeed several scientists are credited with having originated the idea. It is seldom that a scientific theory of importance is the work of one or two men.

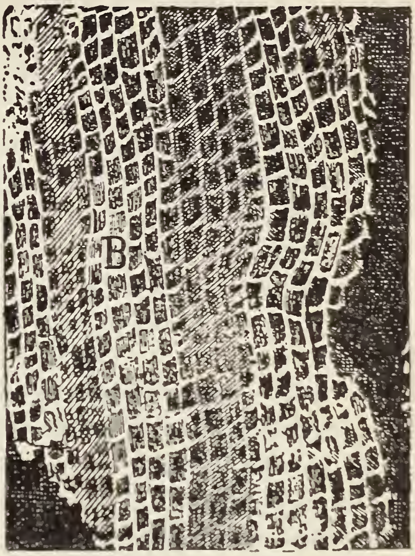

Fig. 4:2 The first published illustration showing the cellular structure of a tissue. A section of a piece of cork as seen by Robert Hooke with his microscope. Reproduction of an illustration in his *Micrographia*, published in 1665. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

We must picture organisms, plants of all kinds including the largest trees and the most delicate flowers, animals from the simple jellyfish to higher forms like the dog, cat, or elephant, and even the human body as made up entirely of small microscopic cells and substances formed by them. Each of these cells carries on its own vital activities, depending, however, to a considerable extent, on the activities of the cells around it.

One may ask, Why, in general, is the protoplasm in a plant or animal partitioned into cells? The question may mean, Is there a physical necessity, protoplasm being what it is, for the partitioning? The answer to this would seem to be that the organization and differentiation found in animals and plants could not exist in any but the smallest or simplest of them if the living material were able to flow freely and at random throughout their bodies. The question may also mean, What advantage or advantages accrue to the organism from the cellular organization?

Among the advantages are (*a*) the opportunity for specialization and differentiation of the cells to form tissues carrying on different functions in the organism such as digestion, contraction, and sensation, and (*b*) the insurance against total injury, since if some of the cells are injured the injury to the living material may be confined to the injured cells.

The importance of the cell principle can scarcely be overemphasized. In all branches of biological science it is becoming more and more evident that "the key to every biological problem must finally be sought in the cell." The cell principle has "opened far-reaching new vistas of progress in physiology and revolutionized our views of vital action, in health and in disease. . . . By force of habit we still continue to speak of the cell 'theory' but it is a theory only in name. In substance it is a comprehensive general statement of fact and as such stands to-day beside the evolution-theory among the foundation-stones of modern biology." [1]

In 1858, twenty years after the announcement of the cell principle, the pathologist Virchow stated a second almost equally important principle in the simple words *Omnis cellula e cellula* — every cell from a cell. Subsequent investigations of the reproduction, growth, and development of plants and animals have firmly established this principle. Further, we now know that a cell gives rise to another cell only by a process of division in which the division of the nucleus precedes the division of the entire cell.

2. CELL DIFFERENTIATION

Except in certain special cases, which need not be discussed at this point, somewhere in its life cycle every plant and every animal exists as a single cell — a fertilized egg cell. When a multicellular organism is formed from this fertilized egg, the cells of the body of the organism are the result of repeated cell division beginning with the division of the fertilized egg cell. The differentiation and specialization of the cells proceed as they multiply and take up their positions in the new organism. In the early embryonic stages of plants and animals the cells are much alike and undifferentiated. As the organs are formed, the cells develop the particular structure peculiar to the cells of the tissue of which they form a part (Fig. 15:1). In all organisms certain cells remain undifferentiated. Some of these cells become the reproductive cells which later develop into eggs or sperm while still others stay ready to take part in the repair of injury, or replacement of parts lost, during the life of the plant or animal. As the cells of an animal or plant become more and more highly differentiated they seem to lose the power to divide so that the more highly differentiated cells such as those of the nervous system do not increase in number after a certain stage (Figs. 36:4 and 36:5).

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[1] Quotations from E. B. Wilson, *The Cell in Development and Heredity*, The Macmillan Company, New York, 1928.

3. THE SHAPES AND SIZES OF CELLS

A. *THE SHAPES OF CELLS*

When cells occur in a tissue they may fit closely together and occupy most of the space available, as occurs, for example, in cork, in the woody tissue of plants, and in the muscle tissue of animals, or the cells may be more or less widely separated, the spaces between them filled with intercellular materials in the form of liquids or solids as in the connective tissue of animals or with air as in the spongy tissue of the leaves of plants. Where the cells are packed closely together the surfaces of adjacent cells form facets with angular boundaries between the cells. In many cases the shape of a cell is clearly related to its function. Covering cells such as the epidermis cells of plants and animals are flattened, thus increasing the surface which is covered. The storage cells of plants and animals are approximately the same dimension in all directions, thus providing maximum volume with minimum surface. Similarly egg cells when without rigid walls and when suspended freely in a liquid tend to become spherical. The cells of plants which conduct the sap and food materials are elongated, increasing the rate of conduction. The muscle fibers of animals are also elongated in this case, increasing the extent of contraction. Cells endowed with movement, such as the white corpuscles of the blood, tend to change their shape. The nerve cells of animals have long, fine branching processes often extending to relatively great distances for the conduction of nerve impulses.

B. *CELL SIZE*

Cells vary greatly in size but in most cases they are microscopic. The unit of microscopic dimensions is the **micron**, designated by the Greek letter μ, and equal to 0.001 millimeter, a millimeter being approximately $\frac{1}{25}$ inch (Fig. 4:3).[1] The diameter of the period at the end of this sentence is approximately 0.5 millimeter or 500μ. The smallest cells are probably those of bacteria. One of the smallest of these is given as 0.15μ in diameter and 0.3μ in length. For the largest cells one must turn to the

[1] For a more detailed discussion and an illustration refer to Chapter 5.

"yolk" of the eggs of the larger birds and reptiles. The yolk attains its full size in the ovary and as it leaves the ovary and before it begins to develop consists of a single cell which may reach several centimeters in diameter. The cells in the tissues of plants and animals are usually small and invisible to the unaided eye. Thus the cells of the leaf of *Elodea* illustrated in Fig. 4:7 average 150 × 40 × 30μ and their nuclei 10μ in diameter. The tissue cells of the human body average 10 to 20μ in diameter. The red corpuscles of the blood are of uniform shape and size and have a diameter of 7.5μ. Large nerve cells may measure over 100μ, not including their nerve processes which may extend for almost 1 meter (39 inches).

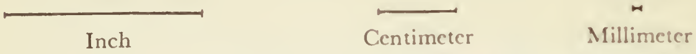

Fig. 4:3 One inch, one centimeter, and one millimeter to show actual sizes.

4. TECHNIQUES FOR THE STUDY OF CELLS

A. *OBSERVATION OF THE LIVING CELL*

Since the chief object in studying cells is to learn how they carry on their living processes, the best technique would be one in which the cells were kept alive under conditions approaching as nearly as possible those in which they spend their normal existence. In the case of plants or animals consisting of a single or only a few cells this can be approximately attained by placing the organism in water, or the liquid in which it lives, on a glass slide and examining it under the microscope. However, when the attempt is made to study the cells of a larger plant or animal, especially those from the interior of its body, difficulties are encountered and special techniques required.

(1) TISSUE CULTURE

Of recent years methods have been devised for keeping the cells of the higher plants and animals alive outside the plant or animal body under conditions in which they grow and multiply. In such cultures the cells can be conveniently observed under the microscope. Most success has been attained by starting with the relatively undifferentiated cells of embryos or young individuals. A culture of cells,[1] obtained from a piece of the heart of an embryo, started by Alexis Carrel in 1912 is still

[1] The cells are fibroblasts, a common type of cell in connective tissue. There is a popular idea that Carrel has kept alive a chicken's heart for 34 years. This is of course not so. What he has kept alive is a culture of some of the relatively undifferentiated cells from an embryo heart.

growing in 1946, that is, 34 years later. The cells grow rapidly, each cell dividing, on an average, twice in 48 hours. The individual characteristics of the tissue are maintained with little variation and the culture has afforded material for numerous investigations.

In the case of the Carrel culture of fibroblasts and similar cultures the cells are kept alive in a culture medium in a glass vessel entirely apart from the animal or the tissue from which they were originally obtained. Such a culture is said to be an *in vitro* (L. *vitrum*, glass) culture.

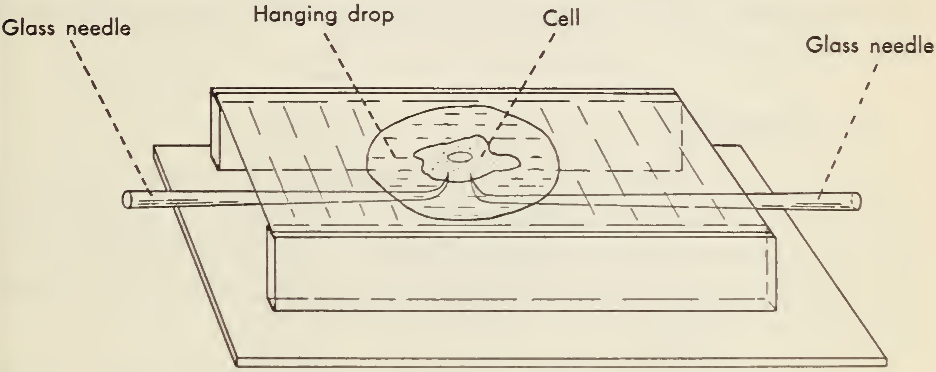

Fig. 4:4 The moist chamber, hanging drop, and needles used in microdissection.

Where this method of culture is unsuccessful or undesirable another method called *in vivo* culture may be used. In this method the cells are cultivated in the tissue of another animal or plant or embryo. The cells to be cultivated are transferred to the other organism under sterile conditions, i.e., conditions which prevent infection, and are implanted in the tissue of the "host" organism, preferably where they can be kept under observation.

(2) MICRODISSECTION

Individual cells are much too small to be handled or dissected by the usual methods. However, a number of different instruments have been devised to move, pierce, cut, and inject cells under the microscope. Such work is called microdissection. Usually the cells are placed in a hanging drop on the underside of a glass slide. One or more very fine glass needles are moved by means of fine screws or levers, or a combination of the two, so as to approach the cells through the underside of the drop (Fig. 4:4). By substituting a very fine glass tube for one of the needles, materials or parts can be sucked from the cell or solutions can be injected into the cell.

B. FIXATION

When a cell dies its structure changes and the protoplasm may disintegrate and dissolve into the surrounding medium. If the structure of the cell is to be preserved, the protoplasm must be killed in such a way as to coagulate it quickly. The protoplasm is then said to be fixed. This may be brought about by heat or by chemicals such as formaldehyde or corrosive sublimate. When the cell has been fixed, it may be preserved in a transparent liquid, or be impregnated with a material such as Canada balsam which becomes a transparent solid, and mounted on a glass slide.

C. STAINING

To make visible differences in the protoplasm or included bodies in the cell, it is frequently necessary to use certain dyes or stains which color some of the structures and not others. Some of these dyes can be used on the living cell and are called **vital stains,** others can be used only on fixed material.

D. SECTIONS

For the study of tissues from different parts of the body it is frequently necessary to make extremely thin sections. A piece of tissue, after being fixed, is infiltrated with paraffin wax or celloidin to make it of a consistency suitable for cutting. The sectioning is done with an exceedingly sharp razor in a special apparatus called a **microtome.** With this technique it is usual to make sections of 3 to 10 μ in thickness which is less than the thickness of the average cell. With special care sections of 1 μ or less can be made. Such sections may be stained and mounted in a transparent material such as Canada balsam. When sections must be made in the shortest possible time, as for diagnosis in pathological laboratories, the tissue may be frozen and sectioned in that form.

5. THE CELL, A GENERAL DESCRIPTION

It is convenient to begin with a general account of the cell. This account will include mention of all of the more important structures occurring in cells, and will facilitate the description of the different types of cells in the sections to follow. Probably no living cell corresponds exactly to this generalized cell and certainly in many cells not all of the structures here described have been seen (Fig. 4:5).

The first part of the cell to be discovered was the **cell wall,** seen first in plant cells. Here the wall is composed usually of a carbohydrate called **cellulose,** but other substances may be incorporated with the cellulose or the cellulose may be replaced by a different compound.

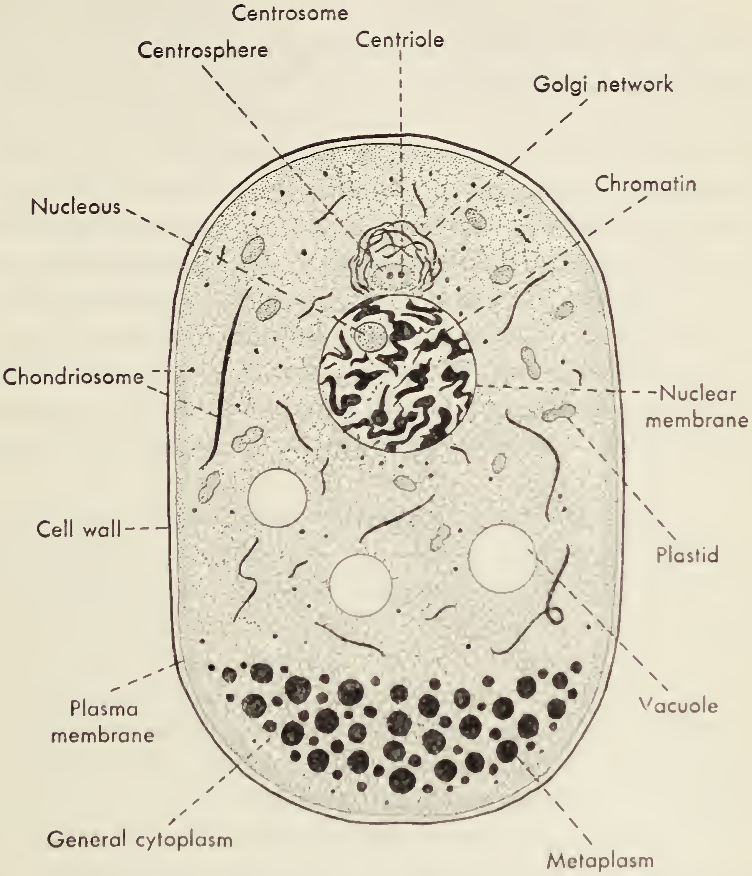

Fig. 4:5 A generalized diagram of a cell. It should be noticed that rarely if ever do all the cell structures shown appear together in the same cell at the same time. After E. B. Wilson, *The Cell*, The Macmillan Company.

Frequently in plant tissues the protoplasm dies and leaves only the cell walls. This is the case in woody tissue, except in the early stages of its formation, and in cork. Animal cells are usually devoid of any rigid outer covering similar to the cellulose walls of plants, although they may be covered with various nonliving membranes and retain a definite shape. In some cases, intercellular substances may be formed so that the individual cells are widely separated. This occurs in cartilage and bone.

The living part of the cell is called the **protoplast.** The protoplast is divided into the **cytosome** (Gr. *kutos*, cell + *soma*, body) and the **nucleus** (plural, *nuclei*, L. a kernel).[1]

A. THE CYTOSOME

The protoplasm of the cytosome is called the **cytoplasm.**[2] The cytoplasm is always surrounded by a **plasma membrane.** This membrane is extremely thin, being probably at most only a few molecules in thickness and is under ordinary circumstances not visible with even the highest powers of the microscope. It is regarded as a portion of the living protoplasm and is not to be confused with the cell wall of plant cells or the nonliving membranes of animal cells with both of which it may be in close contact. Not being visible, its presence can be demonstrated only indirectly. It can be separated from the cell wall in plant cells by plasmolysis, a phenomenon to be described later, but is most clearly demonstrated in microdissection. By this method it can be shown "that the plasma membrane is of firm or even tough consistency, in some cases elastic, and offers considerable resistance to mechanical injury."

The cytoplasm may be differentiated into several types of formed bodies, called **organoids,** which are specialized to perform special functions. Also contained in the cytosome[3] are various nonliving bodies in the form of granules, globules, or crystals, to which the term **metaplasm** (Gr. *meta*, between) may be applied. These consist of stored food material, preliminary stages in the manufacture of secretions, or waste materials. The nature and the finer structure of protoplasm will be discussed in a later chapter. It should, however, be emphasized that protoplasm is not a single chemical substance but a very complicated mixture of a number of different chemical substances and that the chemical substances and the manner in which they occur in the mixture probably differ in each species of animal and plant. Further, the protoplasm of the different cells of the same individual is not exactly the same, nor is the protoplasm the same at all stages in the life of the cell. Activity implies change, and activity is the very essence of life. Under normal conditions the protoplasm of all organisms is in a constant state of flux.

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[1] The question is frequently raised whether there are cells without nuclei or whether a mass of protoplasm without a recognizable nucleus can be called a cell. For example, the human red corpuscles in the peripheral circulation are without nuclei. However, at the time of their origin they are nucleated and they lose their nuclei only when they become specialized as containers of the red pigment haemoglobin which acts as a carrier of oxygen. Another case is that of the cells of bacteria and some of the lower algae. Bacteriologists and microbiologists are not in complete agreement as to what, if any, structure or structures constitute the nucleus in these cells.

[2] The term protoplasm is sometimes used as equivalent to cytoplasm. It seems, however, better to retain it in its original meaning to include all the living material in the cell.

[3] The words "cytosome" and "cytoplasm" are by some authors used synonymously. Here the term cytoplasm is reserved for the living material in the cytosome.

(1) CELL ORGANOIDS

Among the more frequent and important of cell organoids are the following: plastids, chondriosomes, Golgi bodies, vacuoles, fibrillar organoids, and the central bodies.

Plastids (Gr. *plastes*, one who molds) are almost entirely confined to plant cells but are occasionally found in some of the lower animals. They are centers of chemical activity and vary in size and shape. They have been shown to multiply by division within the cell but appear also to arise by differentiation directly from the cytoplasm. Some of them are colorless and are then called **leucoplasts** (Gr. *leukos*, white). The majority are colored by contained pigments and are hence called **chromoplastids**[1] (Gr. *chroma*, color). The commonest chromoplastids are those which contain chlorophyll, the green pigment of plants which plays an important role in the process of photosynthesis, leading to the formation of sugar. These are called **chloroplastids** or **chloroplasts.**

Chondriosomes[2] (Gr. *chondros*, a granule + *soma*, a body) take the form of small granules, rods, or filaments which are found rather generally in both animal and plant cells. They are of low refractive index but can be seen in the living cell. Most characteristic is their reaction to certain stains. Little is known regarding their function.[3]

The **Golgi network**[4] is likewise distinguished by its form and staining reactions. It frequently occurs as a network surrounding or on one side of the nucleus. It has been found in a variety of animal tissues, especially in nerve cells. The function of the Golgi network is apparently related to the fat and protein metabolism of the cell.

In the case of **vacuoles** interest attaches to the surrounding membrane, which would seem somewhat similar to the plasma membrane but formed internally, and to the contents of the vacuole. Vacuoles may contain material to be digested and absorbed into the cytoplasm or they may contain waste products to be extruded.

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[1] The term **chromatophore** (Gr. *phoros*, one who bears) is sometimes used as a synonym for "chromoplastid," but the latter is the better general term since "chromatophore" is used with special reference to the plastids of Algae and is also used for certain pigment cells in animals.

[2] Also called **mitochondria** (Gr. *mitos*, a thread + *chondros*, a granule).

[3] One authority has maintained that they are bacteria.

[4] So named after its discoverer, the Italian neurologist Golgi.

Fibrillar organoids are fibers which extend in a definite direction in the cell and may be supporting, contracting, or conducting elements. Supporting fibrillae are found in flagellate Protozoa and in ciliated cells. Contracting fibrillae are characteristic of muscle fibers, especially striated muscle fibers. Fibrillae occur generally in nerve cells and are probably present in other less specialized cells.

Flagella (L. *flagellum*, a whip) and **cilia** (L. *cilium*, a hair) are long, thin cytoplasmic processes extending outward from the exposed surface of a cell and used either for locomotion or to produce a current of liquid over a surface. The processes are called flagella when they are relatively long and the cell bears only a few of them. They are called cilia when they are relatively short and numerous.[1] Cilia usually beat back and forth in unison, while flagella lash about independently.

The cells of most of the higher animals and of many of the lower animals contain a structure called the **central body** or **centrosome** which is usually located near the nucleus. Frequently the central body contains one, or more often two, deeply staining central portions called **centrioles** surrounded by a faintly staining centrosphere. Central bodies apparently do not occur in the cells of the higher plants. An important, but not the only function, of the central body seems to be the part which it plays in the division of the nucleus. In this connection it will come up for further discussion in a later section.

(2) THE METAPLASM

The metaplasm consists of nonliving materials deposited in the cytoplasm. Its commonest form in plants is starch which is stored in the form of somewhat irregular, usually ovoid granules of varying size. A compound known as glycogen, similar in chemical composition to starch, takes the place of the latter in animals. It may occur in the form of granules or in solution in vacuoles. Proteins may be stored in the form of granules but they usually occur in colloidal suspension, a form to be considered later. In eggs the metaplasm usually takes the form of yolk granules or oil globules. In gland cells the materials, eventually to be secreted, are often first formed in the cell as secretory granules. In some plants crystals, usually of calcium salts, occur. The cell sap in the vacuoles, especially of plant cells, is to be regarded as metaplasmic. It frequently contains pigment. The colors of most fruits are due to pigments dissolved in the cell sap.

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[1] The term cilium is generally used by botanists for both types of processes.

B. THE NUCLEUS

The present description applies to the nucleus only during what is referred to as the **resting stage,**[1] i.e., the stage in which it is not in the process of division. In the living state, the nucleus usually appears as a rounded body, bounded by a delicate **nuclear membrane,** and without visible structure except for the presence of one or more smaller rounded bodies within it called **nucleoli.** Its substance in this state shows the properties of a liquid. When fixed and stained, the coagulated nucleus shows a somewhat complicated structure. In addition to the nucleoli, which may stain deeply, a framework or reticulum becomes evident. The modern conception regards the reticulum as composed of a single substance and attributes the variations in its stainability to different physiological conditions. For this single substance the term **chromatin** has been retained but some authors, to avoid ambiguity, prefer the newer term **Karyotin.**

Some of the functions of the nucleus have been made clear by depriving cells of their nuclei by microdissection or by other methods. Such experiments on plant cells have shown that the formation of the cell wall, the manufacture of food substances and the utilization of food substances in the cell, and the growth of the cytoplasm, while not depending directly on the nucleus, depend for their occurrence on the presence or absence of substances formed in collaboration with the nucelus. Animal cells seem better suited to experimentation. It is possible by using a rather delicate technique to cut an amoeba in two under the microscope so that one part contains the nucleus intact and the other is without a nucleus. In this experiment it is found that the part containing the nucleus continues to live and to carry out all the activities of a normal amoeba, including growth and reproduction. The part without a nucleus does not die immediately but may live for days, carrying on many of the normal activities of an amoeba, sending out pseudopodia, ingesting and digesting food, respiring and responding to stimuli. However, such a portion consisting of cytoplasm only seems to be incapable of growth or of dividing to form new individuals, and in the course of time dies.

[1] Since the nucleus undergoes its most conspicuous changes just previous to and during cell division, the term "resting stage" has been applied to its condition in the period between divisions. Although the nucleus may take an active part in the growth and metabolism of the cell, its most important role is believed to be in the division and reproduction of the cell. However, some biologists prefer to use the term "vegetative stage" in place of "resting stage" to indicate the metabolic activity of the nucleus during this stage.

C. SUMMARY OUTLINE OF CELL STRUCTURE

- The Cell
  - Cell wall
  - Protoplast
    - Cytosome
      - Plasma membrane
      - General cytoplasm
      - Organoids
        - Plastids
          - Leucoplasts
          - Chromoplastids, including
          - Chloroplasts
        - Chondriosomes
        - Golgi network
        - Fibrillar organoids
        - Flagella and Cilia
        - Central body*
    - Nucleus
      - Nuclear membrane
      - Nuclear sap
      - Reticulum
        - Matrix
        - Chromatin
      - Nucleoli
  - Metaplasm

* The central body may be absent or in the nucleus.

6. SOME TYPES OF PLANT CELLS

A considerable number of different kinds of cells occur in plants, and in the higher plants these are arranged to form tissues. Here, however, only a few types of plant cells will be considered and no attempt will be made to cover the subject of plant tissues.

A. CELLS FROM THE LEAF OF ELODEA

A good object in which to study cells is the leaf of *Elodea*. This plant is found in ponds and sluggish water. It is a flowering plant which has adapted itself to life in fresh water and consists of a long branching stem from which flat, lance-shaped leaves arise. Usually the stem is attached to the bottom by a root imbedded in the mud.

When one of these leaves is magnified under the microscope it is immediately seen to be composed of many cells (Fig. 4:6). By focusing the microscope up and down it becomes apparent that the leaf is made up of two layers of cells and that the cells are fitted together somewhat like the bricks in the side of a house. A single cell greatly magnified is shown in Fig. 4:7. It is to be noted that what one actually sees through the microscope is an optical section of the cell. This is really what one would see were the cell cut with a sharp knife and the cut edge observed.

The microscope gives us such an optical section because the lenses bring into view only structures which lie in a single plane at right angles to the direction of vision so that the picture has no depth. Thus the cell wall which completely encloses the cell appears only as an outline. The cell wall is of appreciable thickness and is sufficiently rigid to give to the cell a fixed shape, and porous enough to allow water and other substances to pass freely through it.

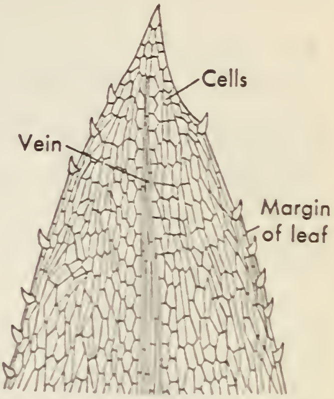

Fig. 4:6 A portion of a leaf of *Elodea* showing the cells of which it is composed. Redrawn after Smith, Overton, *et al.*, *A Textbook of General Botany*, The Macmillan Company.

Inside the cell wall is the protoplasm. Surrounding the protoplasm is a delicate membrane, the plasma membrane which, although indicated in the illustration, cannot be seen under the microscope. The plasma membrane is separate from and quite independent of the cell wall. All materials which are used by the protoplasm in building up its living substance must pass through the plasma membrane, and it is to a large extent the plasma membrane which determines what goes into or comes out of the cell.

In *Elodea* the central portion of the cell is filled by a large vacuole, so that the living protoplasm is in reality restricted to a layer extending between this vacuole and the cell wall. A membrane similar to the plasma membrane, called the **vacuolar membrane,** separates the cytoplasm from the vacuole. The vacuole contains a watery liquid called **cell sap,** containing salts and food substances in solution.

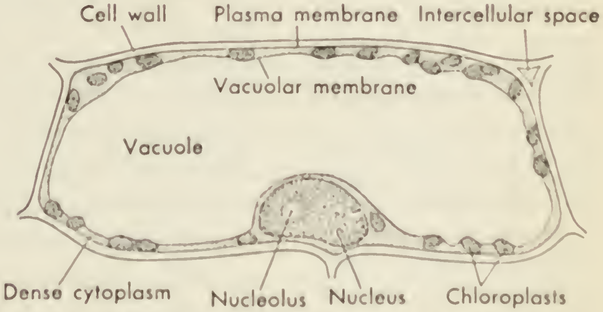

Fig. 4:7 A cell from a leaf of *Elodea.* The plasma membrane lies just within the cell wall and cannot be seen as a separate structure. Redrawn after Smith, Overton *et al.*, *A Textbook of General Botany*, The Macmillan Company.

On one side of the cell and causing the cytoplasm to bulge out into the vacuole is a rounded body, the **nucleus.** This denser portion of the protoplasm is separated from the cytoplasm by a **nuclear membrane.** The nucleus is not always easily seen in living cells on account of other structures in the cytoplasm by which it may be obscured. It often contains a small dense body, the **nucleolus.**

The study of the individual cells shows that the green color of the *Elodea* plant is due to numerous small oval bodies floating in the cytoplasm. These bodies are **chloroplasts** and they are regarded as a living part of the protoplasm; their green color is due to the **chlorophyll.** If one of the chloroplasts already mentioned is watched in a living, active cell it will be seen to move around the cell, up one side, across the end, down the other side, and across the other end, as in dancing an old-time barn dance. The chloroplasts are not themselves motile, they are merely carried along in the cytoplasm which has a streaming movement. This movement of the cytoplasm is called **cyclosis;** it probably helps in distributing materials in the cell.

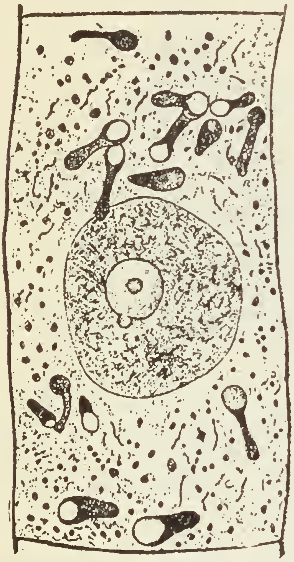

Fig. 4:8 A cell from the embryonic region of the root tip of the garden pea, *Pisum sativum,* showing leucoplasts in different stages of development. The leucoplasts appear as comma-shaped structures containing small colorless starch grains. The granules and fine hair-like structures in the cytoplasm are chondriosomes. From D. M. Mottier, *A Textbook of Botany for College Students,* P. Blakiston's Son & Company, Inc.

B. A CELL FROM THE TIP OF A ROOT

A cell from the root of the garden pea (*Pisum sativum*) will serve to show some of the cytoplasmic inclusions found in cells (Fig. 4:8). Such a cell is colorless and is concerned with the storage rather than the manufacture of food materials. This is indicated by the presence of **leucoplasts** and by the starch grains associated with them. In the cytosome are chondriosomes which have the form of granules and threads. A nucleolus is present in the nucleus. The cell wall is thin and the plasma membrane is not indicated.

C. CELLS OF THE CONDUCTING TISSUE OF A PLANT STEM

A different type of cell is seen in the conducting tissues of plants. One kind of cell through which food material is conducted is called a **sieve tube** (Fig. 4:9). A sieve tube consists of elongated cells, the end walls of which, called **sieve plates,** contain minute perforations through which pass strands of cytoplasm, connecting the protoplast with the protoplast of the cell above and below it. The protoplasts of mature sieve tubes are without nuclei. Their cytoplasm may contain plastids. In some cases, cells called **companion cells** are associated with the sieve tubes. These cells contain nuclei.

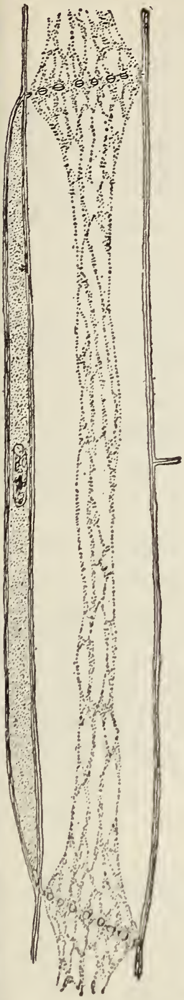

Fig. 4:9 Cells from the conducting tissue of the stem of the tobacco plant, *Nicotina tabacum*, showing on the right a sieve tube and on the left a companion cell. The protoplasm in the sieve tube takes the form of a strand extending from end to end of the cell and is without a nucleus. The protoplast of the long slender companion cell on the left of the sieve tube fills the cell and contains a nucleus. From R. M. Holman and W. W. Robbins, *A Textbook of General Botany*, John Wiley & Sons, Inc.

D. THE CELL OF A SINGLE-CELLED PLANT

The cell of a single-celled alga, *Chlamydomonas*, shows certain features not seen in the previous cells (Fig. 4:10). The entire plant consists of a single cell which swims about in water by means of two large flagella[1] at one end. Near where the flagella join the body are two contractile vacuoles which expel their contents at intervals. Not far from these is an eyespot, containing a red pigment and sensitive to light. There is a single large U-shaped chloroplast containing a starch-forming body called a **pyrenoid.**

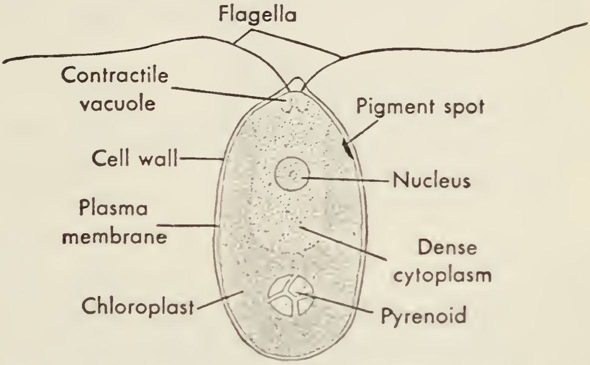

Fig. 4:10 A single-celled plant, *Chlamydomonas angulosa.* From D. M. Mottier, *A Textbook of Botany for College Students*, P. Blakiston's Son & Company, Inc.

7. TYPES OF ANIMAL CELLS

In the higher animals five kinds of fundamental tissues are recognized: epithelial tissue, supporting tissue, muscular tissue, nervous tissue, and vascular tissue. This classification is based on the functions of the cells and the tissues, although with the differences in function are correlated pronounced differences in structure.

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[1] Referred to as cilia in botany texts. See note, p. 98.

A. EPITHELIAL CELLS

Epithelial tissue is essentially a covering tissue. It covers the surface and lines the cavities of the body. A section of the **columnar epithelium** lining the intestine of the mouse will serve as an example (Fig. 4:11). The cells have the shape of irregular tall prisms with their long axes at right angles to the surface of the epithelium. In a section parallel to the surface, each cell appears as an irregular polygon. In a section perpendicular to the surface, the cells are rectangular in outline. The outer surface of each cell is protected by a striated border. The inner ends of the cells abut on a basement membrane. When suitably stained, such cells show mitochondria in both filamentous and granular form.

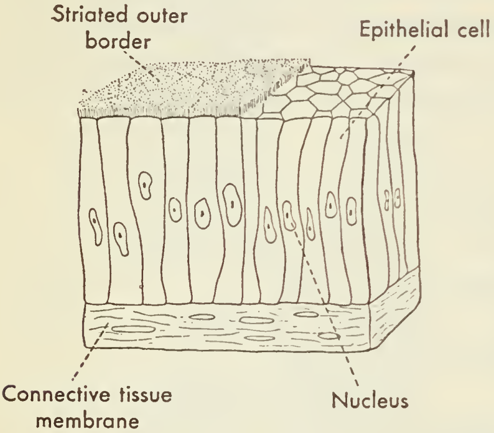

Fig. 4:11 Epithelial cells from the columnar epithelium lining the intestine of the mouse. Redrawn after Maximow and Bloom, *Textbook of Histology*, W. B. Saunders Company.

B. CELLS OF SUPPORTING TISSUES

A thin section of cartilage from the end of one of the leg bones of the frog shows clearly the cells in a supporting tissue (Fig. 4:12A). Separating the cells and formed by them is the stiff jellylike intercellular cartilage substance which gives to cartilage the consistency familiar to all in gristle, which is the common name of cartilage. Cartilage cells have the structure of a typical cell. As the cells grow, the increase in size is followed by cell division and the daughter cells become separated by the formation of more intercellular cartilage substance.

In bone the intercellular substance is made hard by a deposit of calcium carbonate and calcium phosphate. The bone cells are contained in cavities in this bone substance. Connecting these cavities are fine canals. The bone cells which like the cartilage cells have a typical cell structure are put into communication with each other by protoplasmic processes passing through the canals (Fig. 4:12B).

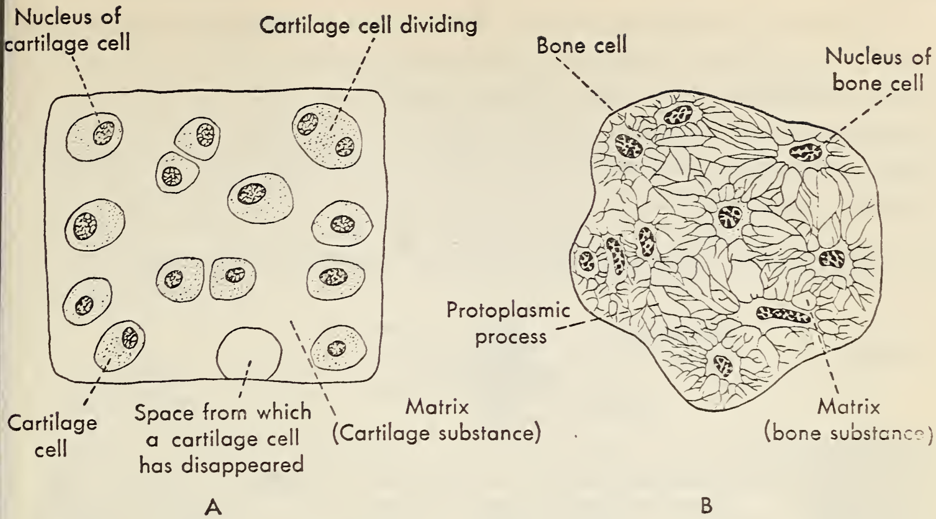

Fig. 4:12 Cells of cartilage and bone. A. Section of a piece of cartilage. B. Section of a piece of bone from a white mouse. B, redrawn after Maximow and Bloom, *Textbook of Histology*, W. B. Saunders Company.

C. MUSCLE FIBERS

In any of the muscular layers of the digestive tract may be found examples of cells differentiated for contraction (Fig. 4:13). Such cells have the form of an elongated spindle and their contained nuclei are also elongated in the direction of their long axes. By special technique fine fibrils running parallel to their long axes can be demonstrated in these cells. Because they lack the transverse striations visible in the voluntary or skeletal muscles, such cells are called **smooth muscle** cells.

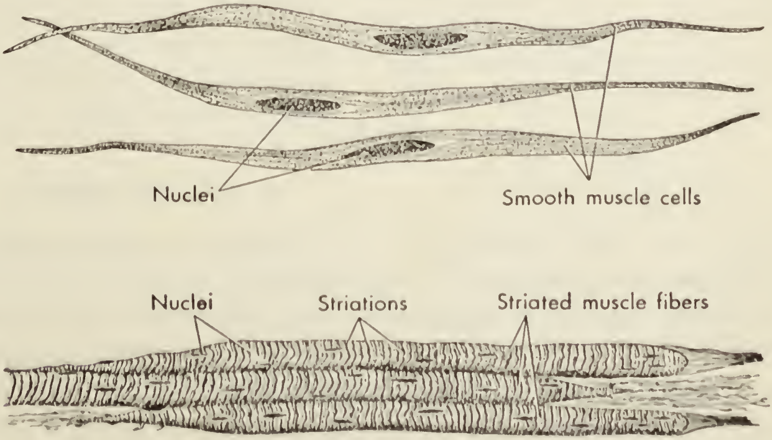

Fig. 4:13 Muscle tissue. Above, smooth muscle cells. Below, striated muscle fibers. Redrawn after Bailey, *Textbook of Histology*, William Wood & Company.

The fibers of voluntary muscle tissue are not in the strict sense cells, since a single fiber contains numerous nuclei and seems to correspond to a number of cells. Fine fibrils extend lengthwise in the muscle fiber. The **striations** which characterize these fibers are in the fibrils and run transversely. Metaplastic glycogen granules are distributed in the cytoplasm between the fibrils.

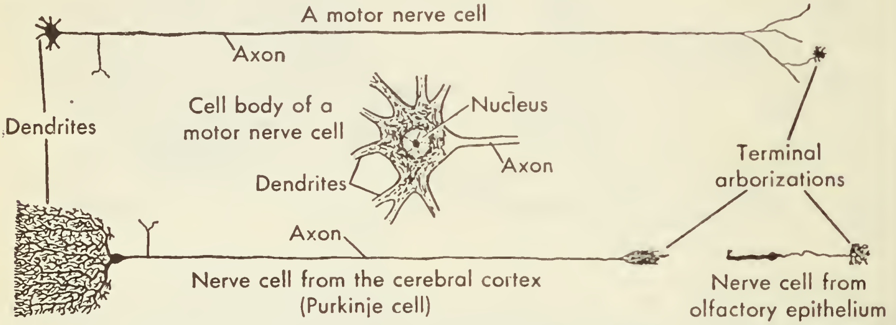
A motor nerve cell
Axon
Dendrites
Cell body of a motor nerve cell
Nucleus
Axon
Dendrites
Terminal arborizations
Axon
Nerve cell from the cerebral cortex (Purkinje cell)
Nerve cell from olfactory epithelium

Fig. 4:14 Various types of nerve cells. Redrawn after Bailey, *Textbook of Histology*, William Wood & Company, publishers.

D. NERVE CELLS

Nerve cells are characterized by long, fine, cytoplasmic processes which conduct the nerve impluses. Nerve cells vary greatly in size and in the length of their processes (Fig. 4:14). Careful observation of the living nerve cell and the employment of suitable staining methods reveal numerous fine fibrils extending through the cytoplasm and into the cytoplasmic processes. The Golgi apparatus is specially well shown in nerve cells.

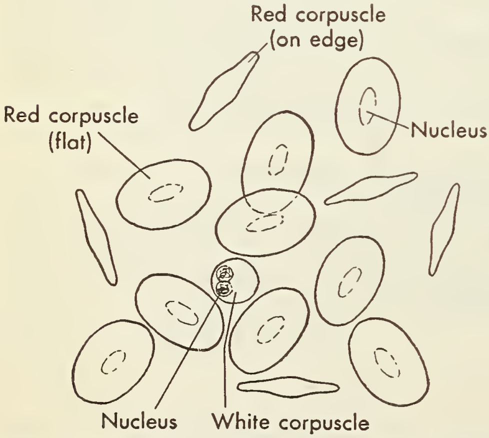

Fig. 4:15 Blood corpuscles of the frog. The red corpuscles of the frog have nuclei.

E. BLOOD CELLS

Blood contains a number of different kinds of cells (Fig. 4:15). By far the most numerous are the **red blood corpuscles.** Different kinds of **white blood corpuscles** occur. These differ in cell size, the relative size and shape of the nuclei, and in the kinds of granules contained in the cytosome. The red corpuscles of the frog are nucleated. In man the red corpuscles lose their nuclei during development.

8. CELL DIVISION

We have already seen that the living cell is an exceedingly complicated structure. We are now to see that the usual process by which cells divide is no less complicated. This is not surprising when one considers that when a cell divides each half receives and preserves the complicated structure of the parent cell. Cell division as ordinarily understood involves two separate events: the division of the nucleus and the division of the cytosome.

A. THE DIVISION OF THE NUCLEUS

The division of the nucleus precedes that of the cytosome. The ordinary method of nuclear division is called **indirect division** or, more usually, **mitosis** to distinguish it from a rare and unusual form called **direct division** or **amitosis.** In amitosis the nucleus merely constricts and divides into two parts. Since amitotic cell division occurs only rarely and is not of general biological interest, it will not be considered further.

(1) THE RESTING NUCLEUS [1]

The resting stage of the nucleus has already been described in an earlier section of this chapter. In the living state it usually approaches the form of a sphere with a sharp outline and an apparently homogeneous interior. By appropriate staining methods a reticulum containing chromatin can be demonstrated and frequently a rounded or irregularly shaped body called the **nucleolus.** As will appear when the process of nuclear division is described the chromatin plays a prominent part and appears to be an essential constituent of any nucleus. On the other hand, the nucleolus or the nucleoli, for there may be more than one, usually disappear as the nucleus begins to divide and new nucleoli are formed in the daughter cells after the division is completed.

(2) MITOSIS

The process of mitosis seems to be chiefly concerned with certain organized bodies known as chromosomes. Although chromosomes have been observed generally in cells only during mitosis, there is considerable evidence that the organization of the nuclear reticulum which they represent exists during the vegetative stage of the nucleus. The chromosomes seem to be formed by a process of condensation from the reticulum. The chief result of mitosis seems to be the division of each of the chromo-

[1] See note, p. 99.

somes into two equal longitudinal halves, in such a way that one of the halves of each chromosome goes into each of the new nuclei formed by the division.

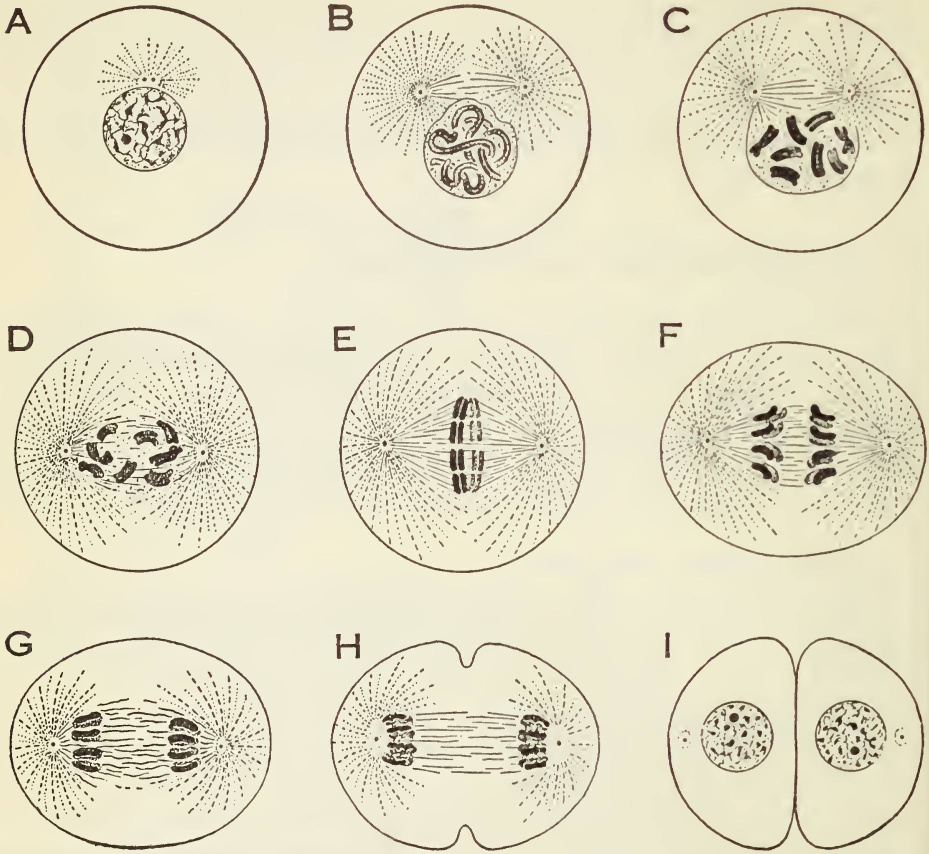

Fig. 4:16 A series of diagrams showing the process of mitosis. The number of chromosomes is assumed to be eight. A. Resting stage or vegetative stage. B. Early prophase. The centrioles have separated and the centrosome has divided and is beginning to form a spindle. Each chromosome consists of two long thin chromatids adhering along their entire length. C. Middle prophase. The chromosomes have contracted. D. Late prophase. The chromosomes have contracted still more. E. Metaphase. The spindle is completely formed and the chromosomes are on the equatorial plate. F. Early anaphase. The chromatids, now chromosomes, are moving apart. G. Late anaphase. The chromosomes are approaching the poles. H. Telophase. The chromosomes are merging to form chromatin networks. I. Mitosis is now complete. Two daughter nuclei have formed and the cytosome has divided. Diagrams from L. L. Woodruff, *Foundations of Biology*, The Macmillan Company.

Important differences occur in the process of mitosis as it occurs in animals and plants and indeed there is great variation between the different species. The object of the present description is to give the main outlines of the process with emphasis on those features which seem to have the most important biological consequences rather than to give details however conspicuous they may be in actual cases.

Mitosis is described as occurring in a number of different phases named, in order, prophase, metaphase, anaphase, and telophase, but it should be understood that the process is continuous and that in the actual division the phases merge into each other (Fig. 4:16).

(a) THE PROPHASE

The beginning of mitosis is characterized by the appearance of long, fine, coiled and contorted threads which usually, but not always, are evenly distributed throughout the nucleus. In the older descriptions of the process the threads were said to be joined end to end to form a spireme. However, more recent observations seem to show that this is definitely not the case, with possibly a few exceptions. These threadlike bodies are the **chromosomes.** In some cases it is possible to see that from its first appearance each chromosome thread consists of two threads closely applied to each other along their entire lengths and it seems probable that this is the rule. Each of these threads into which the chromosome is divided longitudinally is called a **chromatid.** While in most cases the chromosome threads appear to be uniform along their entire lengths, in certain cases each chromosome or each chromatid, when they can be distinguished, is seen to consist of a string of characteristic particles of unequal size and at unequal distances apart. These characteristic granules are called **chromomeres.** When the chromatids and chromomeres can be distinguished in the same preparation the chromomeres in each pair of chromatids are found to correspond exactly in size and position along the chromosome.

As the process of division proceeds each chromosome contracts in length and increases in thickness. Exactly how this occurs is not clear but there is some evidence that it is due to the chromosome assuming the form of a tightly coiled spiral. By the end of the prophase the chromosomes are a tenth to a twentieth of their original length and the differentiation into chromatids and chromomeres is usually no longer visible.

(b) THE METAPHASE

The metaphase is characterized by the formation of a new structure, the **spindle,** and by the arrangement of the chromosomes in this spindle preparatory to the separation of their chromatids. The spindle has the shape which its name implies and seems to be of a somewhat firmer consistency than the surrounding protoplasm. It seems to vary in its method of origin. Usually in the higher animals and plants, the nuclear membrane breaks down and the spindle forms in the region previously occupied by the nucleus. When a **centrosome** is present in the cytoplasm this divides and the two **centrioles** move apart and come to be located at the poles of the spindle. When no centrosome is present, as in higher plants, their place seems to be taken by two **polar caps** which form in the cytoplasm in positions corresponding to the poles of the spindle before the nuclear membrane breaks down. Midway between the two poles of the spindle and extending at right angles to the axis joining these two poles is the **equatorial plate.** This is a region rather than a differentiated structure. The circular area where the equatorial plate meets the outer portion of the spindle may be called the **equator of the spindle.**

In the metaphase, the chromosomes, which in general are scattered fairly uniformly throughout the nucleus in the prophase, take up positions in the equatorial plate. The positions which the chromosomes occupy seem to depend on a certain point in each chromosome, called the **point of attachment,** being in the equator of the spindle. The portions on either side of the point of attachment of a chromosome tend to form a V. These portions may lie entirely outside the spindle as is the case in many animals or they may lie inside the spindle as in many plants. In fixed and stained material the spindle seems to show a fibrillar structure, fibrillae extending from pole to pole. These fibers are called **spindle fibers.** It is generally believed that the chromosomes become attached to spindle fibers and that the attachment is to the centromeres of the chromatids.

(c) THE ANAPHASE

At the end of the metaphase the two chromatids of each chromosome are still in contact along their entire length. At the beginning of the anaphase they begin to separate at the point of attachment and the separation gradually extends along each chromosome to reach the ends. Before the separation of the chromatids of each chromosome is complete they may remain, for a short time, connected so as to give the appearance of two V's attached at their upper ends. The separation of the chromatids and their movement to opposite poles of the spindle is believed to be due to the shortening of the spindle fibers to which they are attached. After the separation is complete the chromatids, now called daughter chromosomes, move toward opposite poles of the spindle.

(d) THE TELOPHASE

During the telophase the chromosomes go through a series of changes which seem to be, in general outline, the reverse of those which they go through in the prophase. The result is the formation of two daughter nuclei surrounded by nuclear membranes, each in the resting stage and exactly similar to the nucleus from which they arose. If centrosomes are present one persists with each of the daughter nuclei. Usually the centriole in each centrosome divides toward the end of the telophase to form the pair of centrioles present in the resting stage.

With the formation of the daughter nuclei the spindle disappears completely in animal cells. In plant cells the spindle in the equatorial plate region, beginning in the anaphase, becomes transformed into a cell plate which eventually extends across the entire cell and forms the new cell wall separating the cells.

B. DIVISION OF THE CYTOSOME

The division of the cytosome follows that of the nucleus. In animal cells the division usually starts on the outer surface as a furrow in the plasma membrane which extends around the cell in a plane at right angles to the axis of the spindle and gradually deepens so as ultimately to divide the cell. After the division the surfaces of the two cells may flatten against each other. As already explained, in most plant cells the division of the cytosome is achieved by the formation of the cell plate and is thus usually closely related to the division of the nucleus.

C. SOME GENERAL CONSIDERATIONS

It should be emphasized that the process of cell division in one or other of the forms outlined is of almost universal occurrence in plants and animals and occurs whenever a cell divides. A cell can give rise to another cell only by cell division preceded by nuclear division. Except, as already stated, for the comparatively rare occurrence of amitotic or direct division, nuclear division is always in the form of mitosis, and essentially similar to that already described.

Cell division in a typical plant cell differs from that in a typical animal cell chiefly in the absence of a central body and the fact that the spindle contributes to the formation of the new cell wall. So far as the division of the chromosomes, the essential part of the process, is concerned, the two methods are fundamentally the same.

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Questions

1. Define the term "protoplast." Account for the meaning which has come to be attached to the word "cell" in biology.
2. Discuss the advantages to an organism of the cellular type of organization.
3. Account for the different shapes of the cells in plant and animal tissues.
4. Try to picture to yourself the size of a red blood cell and the size of a cell

from a leaf of *Elodea*, using for comparison some familiar small object such as the end of a pencil lead.

5. Discuss different techniques for the study of cells including: tissue culture, microdissection, fixation and staining, and sectioning.
6. Discuss differences between the cell wall and the plasma membrane.
7. List types of cell organoids. Distinguish between cell organoid and metaplasm.
8. Discuss functions of the nucleus.
9. Describe the actual structure of some plant and animal cells.
10. Compare cell division in a higher plant cell and a higher animal. Why is the process so complicated?

Suggestions for Further Reading

Wilson, E. B., *The Cell in Development and Inheritance*, The Macmillan Company, New York, 1925.

Elwyn, Adolph, and Oliver S. Strong, *Bailey's Textbook of Histology*, William Wood & Company, The Williams & Wilkins Company, Baltimore, 1932, Chaps. 1–9.

Sharp, Lister W., *An Introduction to Cytology*, McGraw-Hill Book Company, Inc., New York, 1937.

CHAPTER 5

Chemical Elements and Inorganic Compounds

Biology seeks to find a scientific explanation of the structure and activities of protoplasm in terms of known physical and chemical facts and principles. In order to follow this explanation, it is necessary to have clearly in mind certain fundamental physical and chemical ideas.

1. MATTER

All organisms are composed of matter. Matter as defined by the physicist is whatever occupies space, be it solid, liquid, or gas. When we say that organisms are composed of matter it is the matter of the physicist that we mean.

A. THE INDESTRUCTIBILITY OF MATTER

The matter of the earth and all that exists upon it is believed, under all ordinary conditions, to be indestructible. This is expressed as the **law of the conservation of matter.**[1] Matter of one or more kinds can be changed into matter of another kind as happens when water becomes ice or when coal is burned. The weight of the ice formed is exactly the same as the weight of the water which was frozen. In the case of the coal the matter not turned into ash disappears in the form of smoke and invisible gases. Nevertheless, when all of the matter concerned in the process is collected and weighed it is found that the total weight of this matter before the combustion, including the oxygen from the atmosphere which combined with the carbon in the coal, is, in this case also, exactly equal to the total weight of the products of combustion.

All of the evidence now available seems to show that the law of the conservation of mass applies equally to living and nonliving matter.

[1] There is good evidence that under certain special conditions matter may be transformed into energy and energy transformed into matter. But this need not concern us here.

B. CHEMICAL SUBSTANCES

Water and coal may be considered to be chemical substances.[1] A **chemical substance** is a portion of matter which is uniform throughout its mass so far as concerns the properties which characterize it as a particular substance. This means that no matter how the substance may be divided up into smaller portions each of these portions will have the properties of the substance. Ice and water are different states of the same substance. (States of matter are discussed in a later section.) The number of different known substances is very great, probably well over a quarter of a million, and there are certainly many substances which are not yet known.

In nature most matter is in the form of mixtures of chemical substances. Thus a clod of soil contains a great many different substances, too numerous to name. The atmosphere is a mixture of a number of different gases. A **mixture** is made up of two or more substances, each of which retains its own properties. The composition of a mixture may vary and usually the constituents may be present in almost any proportion.

Chemists have found that most of the vast number of known substances can be decomposed into simpler substances but that a few cannot be so decomposed. These latter substances, which seem to be the primary materials out of which the others are formed, are called **elements.** There is reason to believe that the number of elements is approximately ninety-two. Depending on their properties, the elements can be arranged in a series in which each element finds a definite place. Substances which can be decomposed into elements are called **compounds.** Thus water can be decomposed into two gases, oxygen and hydrogen, and is, therefore, a chemical compound. Neither oxygen nor hydrogen can be broken up into simpler substances and they are therefore considered to be elements.

A compound differs from a mixture of elements. In a compound the elements are in definite proportions. Thus water contains by weight eight times as much oxygen as hydrogen. The properties of a compound are quite definite and different from those of the elements which compose it. Thus hydrogen and oxygen are gases at ordinary temperatures, but water which they combine to form is a liquid. The water vapor which is formed when water boils is a gas but it is very different from either hydrogen or oxygen.

---

[1] As ordinarily encountered neither of these is a chemically pure substance, but chemically pure substances are very rarely encountered in nature.

C. THE STRUCTURE OF MATTER

The nature and behavior of chemical substances can be clearly explained only when their structure is understood. The units of matter from the chemical point of view are the **atoms.** There are as many different kinds of atoms as there are elementary substances. The nature and structure of atoms will come in for more detailed discussion later. For the present it is enough to regard atoms as minute bodies which give to the elements their specific characteristics. An element or elementary substance may be defined as a substance which is composed of only one kind of atom, the atoms being the atoms of the particular element.

Atoms unite to form **molecules.** This may occur in an elementary substance. Thus oxygen as it usually occurs in the atmosphere consists of molecules each consisting of two atoms. Compound substances always consist of molecules and the molecules consist of at least two different kinds of atoms, viz., the atoms of the elementary substances which have combined to form them. The molecule of water contains two atoms of hydrogen and one atom of oxygen.

The atoms of the chemical elements are indicated by symbols. Usually the first letter or the first two letters of the English name of the element is chosen as the symbol. Thus the symbol for hydrogen is H and that for oxygen is O. However, in some cases the symbol is chosen from the Latin name of the element. Thus the symbol for potassium, the Latin name of which is *kalium*, is K, and the symbol for iron, the Latin name of which is *ferrum*, is Fe.

D. THE ELEMENTS MOST COMMONLY FOUND IN ORGANISMS

Ninety-nine per cent of the material which constitutes protoplasm is made up of the four elements, oxygen, hydrogen, carbon, and nitrogen. The remaining 1 per cent is composed almost entirely of eight other elements, five of which appear to be essential to life. These five are sulphur, phosphorus, potassium, iron, and magnesium. Of the remaining three which occur in appreciable amounts, calcium seems not to be essential to certain of the lower organisms, while sodium and chlorine are not essential for most plants (Table 5:1, Fig. 5:1).

No chemical elements are known which are entirely confined to organisms. It is to be noted, however, that of the four elements most abundant in protoplasm, three, hydrogen, carbon, and nitrogen, are not especially abundant in the earth's crust and one of these, hydrogen, occurs almost entirely combined with oxygen to form water, while most of the nitrogen is in the atmosphere. Most of the carbon on or near the surface of the earth occurs either in organisms, in the products of their activities, or in their remains. Nevertheless, a handful of soil, a glass of water, and a breath of air provide all of the chemical elements necessary for the growth and development of any organism whether it be a bacterium, moss, a tree, an amoeba, an insect, or a man;[2] but of course not in the proportions nor in the chemical combinations needed.

TABLE 5:1. THE OCCURRENCE OF THE ELEMENTS MORE COMMONLY FOUND IN PROTOPLASM COMPARED WITH THEIR OCCURRENCE IN THE EARTH'S CRUST, INCLUDING THE HYDROSPHERE AND ATMOSPHERE, IN PER CENT BY WEIGHT. THE HYDROSPHERE INCLUDES ALL THE OCEANS AND OTHER BODIES OF FRESH OR SALT WATER

	ELEMENT	SYMBOL	PER CENT IN PROTOPLASM	PER CENT IN 10-MILE CRUST, INCLUDING THE HYDROSPHERE AND ATMOSPHERE[1]
Essential* to all organisms	Oxygen	O	76.0	49.52
	Carbon	C	10.5	0.09
	Hydrogen	H	10.0	0.88
	Nitrogen	N	2.5	0.03
	Phosphorus	P	0.3	0.12
	Potassium	K	0.3	2.40
	Sulphur	S	0.2	0.05
	Iron	Fe	0.01	4.70
	Magnesium	Mg	0.02	1.94
Not essential in lower organisms	Calcium	Ca	0.02	3.39
Not essential in plants	Chlorine	Cl	0.10	0.19
	Sodium	Na	0.05	2.64
Extremely rare in protoplasm	Silicon	Si	—	25.75
	Aluminum	Al	—	7.51
			100.00	99.21

* Recent investigations indicate that small quantities of boron, aluminum, silicon, chlorine, manganese, copper, and zinc have a marked effect on the growth of plants and should perhaps be considered as essential elements.

It is to be emphasized that we are considering here only the chemical elements which compose protoplasm and are not taking into consideration the ways in which these elements are combined into compounds in the living protoplast. Furthermore, it should be mentioned that although the proportions in which the elements occur is nearly the same in the protoplasm of all organisms, the protoplasms of organisms differ.

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[1] From F. W. Clark and H. S. Washington, U. S. Geological Survey, Professional Paper 127, 1924, p. 34.

[2] Paraphrased from D. T. MacDougal, *The Green Leaf.*

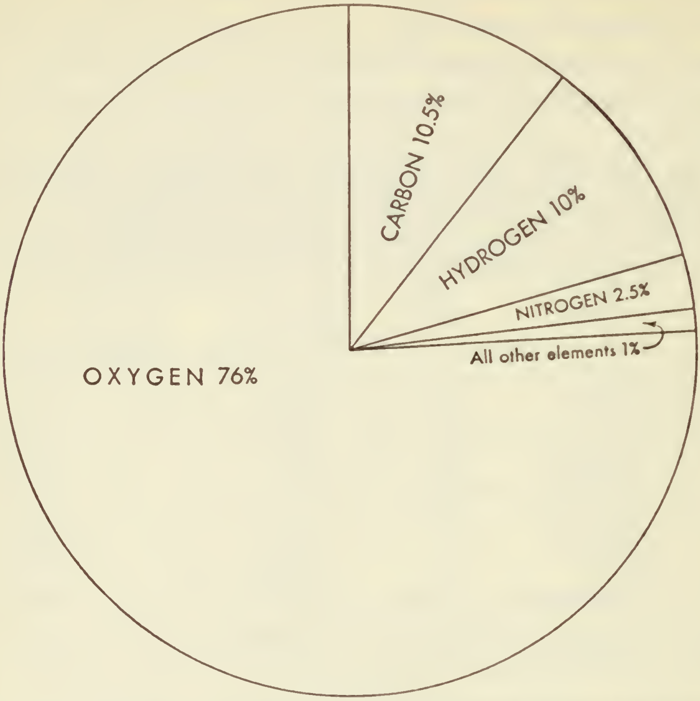

Fig. 5:1 Diagram showing the proportions by weight in which the elements oxygen, carbon, hydrogen, and nitrogen occur in protoplasm.

Indeed each species of organism and probably each individual organism has its own particular protoplasm.

E. THE SOURCES OF THE ELEMENTS IN PROTOPLASM

The chemical elements in protoplasm come originally from the crust of the earth, including the soil; from the hydrosphere which includes the fresh water of the soil, rivers, and lakes, and the salt water of the oceans; and from the atmosphere (Table 5:1, Fig. 5:2). The solid crust of the earth consists of soil and rock. The **soil** is formed by the disintegration of the rocks. Rocks in turn consist of minerals. A given rock may contain one or more minerals. **Mineral** is the term given by the geologist to a chemical compound formed by inorganic processes which takes part in the formation of a rock. This definition excludes such substances as coal and amber which are products of organic activity. A list of the more common minerals and their occurrence in the earth's crust is given in Table 5:2.

The **water of the soil** contains salts formed from the minerals. The salts in the water of the oceans are the result of accumulation through

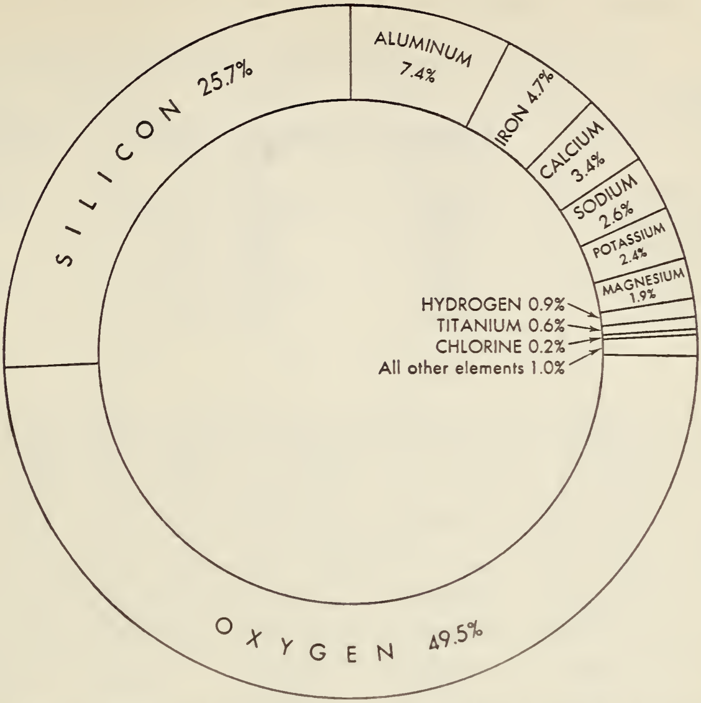

Fig. 5:2 Diagram illustrating the proportion by weight in which the more commonly occurring chemical elements occur in a layer of the earth's crust 10 miles in thickness.

TABLE 5:2.[1] OCCURRENCE OF THE MINERALS IN THE EARTH'S CRUST. AVERAGE COMPOSITION OF A 10-MILE LAYER OF THE LITHOSPHERE

MINERAL	SYMBOL	PER CENT
Silicon dioxide	SiO_2	59.07
Aluminum oxide	Al_2O_3	15.22
Ferric oxide	Fe_2O_3	3.10
Ferrous oxide	FeO	3.71
Magnesium oxide	MgO	3.45
Calcium oxide	CaO	5.10
Sodium oxide	Na_2O	3.71
Potassium oxide	K_2O	3.11
Water	H_2O	1.30
Titanium dioxide	TiO_2	1.03
Carbon dioxide	CO_2	.35
Phosphorus pentoxide	P_2O_6	.30
Chlorine	Cl	.05
Fluorine	F	.03
Other substances		.47
		100.00

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[1] From F. W. Clark and H. S. Washington, U. S. Geological Survey, Professional Paper 127, 1924.

geological time of the salts carried in the soil water to the ocean by the rivers. The salts in the ocean water and the proportion in which they occur are listed in Table 5:3.

TABLE 5:3.[1] PROPORTION IN WHICH THE DIFFERENT SALTS OCCUR IN THE OCEAN

SALT	COMPOSITION OF THE OCEAN SALTS		PER CENT OF TOTAL SALTS
	Formula	Ions formed	
Sodium chloride	$NaCl$	(Na^{+}, Cl^{-})	77.76
Magnesium chloride	$MgCl_2$	$(Mg^{++}, 2\ Cl^{-})$	10.88
Magnesium sulphate	$MgSO_4$	$(Mg^{++}, SO_4^{=})$	4.74
Calcium sulphate	$CaSO_4$	$(Ca^{++}, SO_4^{=})$	3.60
Potassium sulphate	K_2SO_4	$(2\ K^{+}, SO_4^{=})$	2.46
Calcium carbonate	$CaCO_3$	$(Ca^{++}, CO_3^{=})$	.34
Other salts			.22
			100.00

It will be noticed that the elements in the earth's crust, with the exception of some of the iron and of the gases chlorine and fluorine, are all completely oxidized, i.e., they have combined with all the oxygen with which they are capable of combining. In this form they are unable to yield any appreciable amount of energy. The same is largely true of the elements in the ocean, which is to be expected since they are dissolved from the rocks. Hence, in general, organisms, and man is here included, must be dependent ultimately for energy on the sun's radiation, or energy stored up as a result of this radiation.[2]

F. THE SIZES OF THINGS

Size is important in a number of ways. It is difficult to obtain a mental picture of anything without first knowing its approximate size. The rate and course of most processes and energy changes depend on the size or weight of the bodies taking part in them.

The accepted unit of length in scientific work is the **meter** (abbreviation, m).[3] One reason why the meter was chosen is that it is an easily comprehensible length, being a little more than half the height of the average man. One meter equals approximately 39 inches. But the great advantage of the metric system is that larger and smaller units are obtained by multiplying the fundamental unit by powers of 10. This greatly simplifies the arithmetic involved in comparing measurements.

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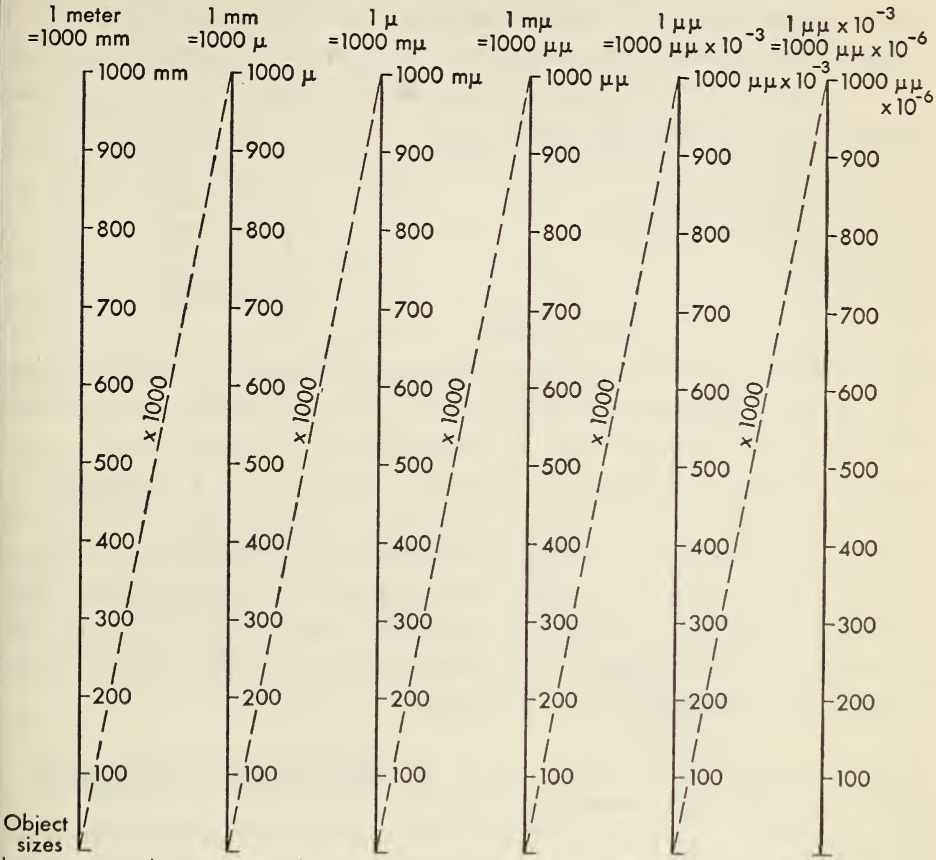
[1] From F. W. Clark and H. S. Washington, U. S. Geological Survey, Professional Paper 127, 1924, p. 33.

[2] As this manuscript goes to press, man seems to be about to enter the "atomic age." When and if this occurs other sources of energy will be available.

[3] The centimeter is the unit of the "C.G.S." or centimeter-gram-second system of the physical sciences. However, both historically and from a practical and theoretical point of view the meter is the fundamental unit.

A centimeter (abbreviation, cm) is 1/100 meter or .01 meter or 10^{-2} meter.[1] A **millimeter** (abbreviation mm) is 1/1000 or 10^{-3} meter (Fig. 5:3). This is about as far as we go in ordinary everyday measurements of length, since 1 millimeter or about 1/25 inch is about the small-



Macroscopic	Microscopic	Colloidal	Molecular	Electronic	Protonic
50 m to .05 mm Multicellular plants and animals	50 μ to .25 μ Cells smallest visible particle =200 μ	Particles 200 μ to 5 mμ	Molecules 5 mμ to .2 mμ Atoms .6 mμ to .1 mμ	Electron 1 μμ x 10^{-3}	Proton 1 μμ x 10^{-6}

Fig. 5:3 Diagram illustrating the units of length used in measuring small objects. On the left the meter is represented by a line 10 centimeters in height, i.e., one tenth its actual height. On this scale 1 millimeter would be represented by the thickness of a very fine line just visible. When, on this scale, the millimeter as represented is multiplied by 1000 the second line to the left is obtained. On this scale, the micron would be represented by the thickness of a very fine line just visible. This method of magnification is continued to obtain the third, fourth, fifth, and sixth lines to the left, the scale being increased each time one thousand fold.

---

[1] The simplest way to express very large or very small numbers is in powers of 10. Thus $1000 = 10^3$, $1{,}000{,}000 = 10^6$, $1/1000 = 10^{-3}$, $1/1{,}000{,}000 = 10^{-6}$. This method is not only less cumbersome and easier to read, but it simplifies the comparison of numbers.

est unit that can be used without special instruments. In measuring cells and other microscopic objects the unit used is the micron, indicated by the Greek letter μ, pronounced mu. The **micron** is 1/1000 of a millimeter or $1\ \mu = 10^{-3}$ mm (Fig. 5:3). To be visible to the unaided eye a particle must be at least 50 μ in diameter. Cells vary greatly in size, but perhaps 50 μ is not far from an average dimension. In measuring molecules or atoms the unit used is the **millimicron**, indicated by mμ. $1\ \text{m}\mu = 10^{-3}\ \mu = 10^{-6}$ mm.[1] The diameters of atoms do not vary greatly and average about 0.1 to 0.4 mμ or 1. to $4. \times 10^{-1}$ mμ = 1 to 4×10^{-7} mm. A still smaller unit, the **micromicron**, indicated by $\mu\mu$, pronounced mumu, is equal to 1/1000 mμ. Thus $1\ \mu\mu = 1 \times 10^{-3}\ \text{m}\mu = 1 \times 10^{-6}\ \mu = 1 \times 10^{-9}\ \text{mm} = 1 \times 10^{-12}$ m. (Table 5:4). It may be noted that the diameter of a human red corpuscle is approximately one thousand times that of one of the hemoglobin molecules which it contains.

TABLE 5:4. THE APPROXIMATE SIZES OF SOME SMALL OBJECTS

The dot on this "i"	0.3 mm	$3. \times 10^{-1}$ mm
A human red blood corpuscle	7. μ	$7. \times 10^{-3}$ mm
A protein molecule (hemoglobin)	6. mμ	$6. \times 10^{-6}$ mm
An oxygen atom	0.13 mμ	1.3×10^{-7} mm
The electron		$3. \times 10^{-9}$ mm
The proton		$2. \times 10^{-12}$ mm

$1\ \text{m}\mu = 10^{-6}$ mm

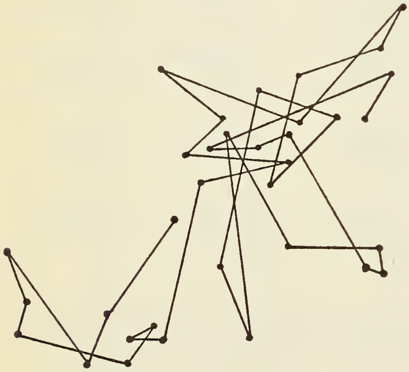


Fig. 5:4 The course taken by a particle in Brownian movement. The lines between the dots represent the distance and direction of the movement in each vibration. After Perrin.

G. BROWNIAN MOVEMENT

If one of the granules in the cytoplasm of a living cell be observed it will be found to be continually moving. If the granule is a fairly large one, the movement will be little more than an irregular vibration, but if it is sufficiently small, 0.5 μ or less, it will go first in one direction then in another in a zigzag course, which, however, does not appear to lead it anywhere since it usually stays near the same spot (Fig. 5:4). The phenomenon is called **Brownian movement,** after its discoverer, Robert Brown, also known as the discoverer of the nucleus of the cell. It is not, as might have been at first supposed, particularly associated with living protoplasm. Precisely the same kind of movement can be seen in sufficiently small granules of almost any material. Experiments have shown that the movement is not due to currents in the liquid.

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[1] Another unit called the Ångstrom unit equal to 1/10 mμ is frequently used.

The most satisfactory explanation is that the movement of the granules is due to their bombardment by the molecules of the water. The molecules of the water are much too small to be seen by the highest magnification of the microscope, but they move with great speed and the force with which they hit the much larger, suspended particles is sufficient to cause the latter to move. Brownian movement provides concrete evidence of the existence of molecules. Other evidence will be advanced later.

If the granule observed in Brownian movement was of such a size as to be just visible with the highest powers of the microscope its diameter may have been about 0.2 μ. Some idea of the size of a molecule, or rather the space occupied by a molecule, compared to the size of such a particle, may be gained from the fact that the particle, if it were water, would contain approximately 6.8×10^7 or 68,000,000 molecules.

2. ENERGY

Energy is defined as the capacity to do work. This work may produce a change in state or a change in position. Thus to change a given amount of ice into water requires a certain amount of heat energy and for a man to walk up a flight of stairs and thus change his distance from the center of the earth also requires an amount of energy depending on his weight and the height of the stairway.

Energy occurs in a number of different forms, including heat, light, sound, chemical energy, and energy of movement. Practically all forms of energy, with the exception of radiant energy, can be classified as either kinetic or potential. **Kinetic energy** is energy of motion, and the kinetic energy of a body is defined as its ability to do work by virtue of its motion. Thus a wheel rotating freely on an axle possesses kinetic energy and may be made to do a certain amount of work before it stops. The **potential energy** of a body is defined as the energy which it possesses by virtue of its position or state. Thus a weight which has been lifted will yield a certain amount of energy when it is lowered, and a coiled watch spring will yield energy when it is allowed to uncoil. Coal possesses potential energy by virtue of its chemical state, and it will give up some of this energy as heat when allowed to combine with oxygen (i.e., burn).

Kinetic energy may be divided into different types depending on the kind of matter which is in motion. In the kinetic energy of **mass movement** entire bodies are in motion. An example is the rotating wheel referred to above. The movement of molecules described in the section on Brownian movement is not confined to water molecules. Indeed the molecules of all substances are in constant movement[1] and it is this movement which is called **heat.** When the temperature of a body is high the movement of its molecules is rapid, and it is said to contain a large amount of heat. When the temperature is low the movement of the molecules is slow, and the body is said to contain little heat.

Potential energy may be classified according to the forces which are involved. The height of a body above the surface of the earth, or more accurately its distance from the center of gravity of the earth, gives it potential energy due to the gravitational force. The potential energy of a stretched or compressed spring or piece of rubber is due to the strain under which the steel or rubber is placed and the tendency of these materials to return to their original condition. The potential energy of chemical substances is really due to the relative positions of the atoms of which they are composed. Thus the existence of the potential energy which we value in coal is due to the carbon atoms in the coal being separated from the oxygen atoms in the air. When these atoms combine to form carbon dioxide the potential energy is released and transformed into heat, a form of kinetic energy.

One kind of energy can be transformed into another. Green plants transform the radiant energy of sunlight into chemical potential energy by forming sugar. When this sugar is eaten by man or any other animal it is changed chemically into another compound, also possessing chemical energy. If, now, the man winds a victrola, some of the potential chemical energy stored up in his body is transformed into potential energy in the compressed spring. When the motor of the victrola is released this potential energy in the spring is transformed to kinetic energy in the rotating table. Some of this kinetic energy is transformed through the needle and the diaphragm into sound which, as a vibrating movement of the air, is another form of energy. Further, transformations could be listed as the sound is received in the man's ear and transferred to his brain, but the attempt to trace these had better be left until after the ear and the nervous system have been discussed.

Since practically all forms of energy can be transformed into heat, energy is frequently expressed in the form of heat (Fig. 5:5). The unit of measurement for heat energy, called the **gram calorie,** is defined as the amount of energy required to raise the temperature of 1 gram of water from 15° to 16° Centigrade. Because this is a rather small amount of energy compared to the amounts involved in most of our everyday activities the **kilogram calorie** is used. This is equal to one thousand times the gram calorie, or the amount of energy required to raise 1 kilogram of water from 15° to 16° Centigrade. In dietetics the energy values of foods are usually expressed in kilogram calories.

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[1] Presumably this movement ceases at the absolute zero of temperature.

Just as there is a law of the conservation of matter, so there is a **law of the conservation of energy.** This law states that energy may be changed from one form to another but it is never created or destroyed.[1]

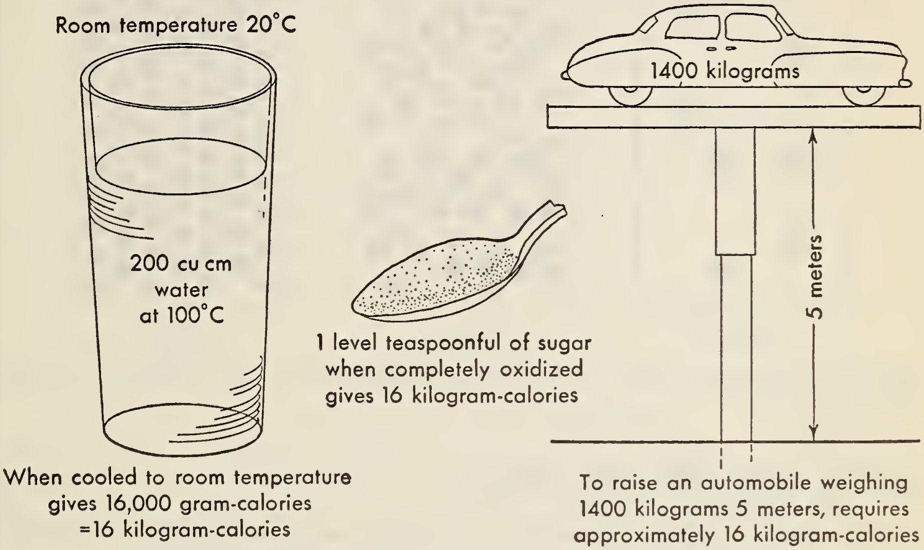
Room temperature 20°C
200 cu cm water at 100°C
When cooled to room temperature gives 16,000 gram-calories =16 kilogram-calories
1 level teaspoonful of sugar when completely oxidized gives 16 kilogram-calories
1400 kilograms
5 meters
To raise an automobile weighing 1400 kilograms 5 meters, requires approximately 16 kilogram-calories

Fig. 5:5 Diagram to show the effect of transforming 16 kilogram-calories into different forms of energy.

All the evidence available seems to show that the laws of the conservation of energy apply to all living phenomena. Most biologists are therefore unwilling to admit the existence of any vital force or vital principle.

3. SOLIDS, LIQUIDS, AND GASES

In a **solid** the attractive forces between the molecules are so strong and the amount of movement due to heat so slight that the shape and volume of the mass remains constant, provided the temperature does not change. When the temperature is increased to the point where the solid melts and becomes a liquid, the heat energy which has been added to it finds expression in an increased movement of the molecules to the point where they may glide over each other and allow the **liquid** to flow but not to change very much in volume (Fig. 5:6). When the temperature is raised still further, to the point where the liquid boils, the increased heat causes the molecules to move to such an extent that they are no longer held together, but journey off into space forming a **gas** which will occupy any volume to which it has access. The pressure which a gas exerts on the walls containing it is due to the bombardment of the walls by the molecules of the gas.

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[1] See note on p. 114.

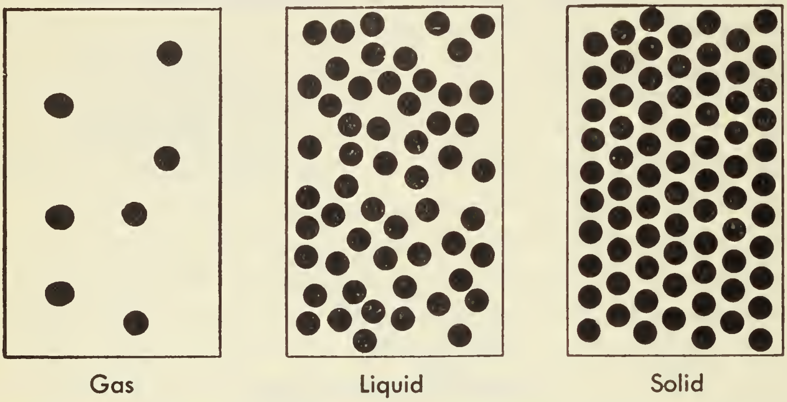


Fig. 5:6 Diagrams to show the density and distribution of the molecules in a gas, liquid, and solid.

4. THE STRUCTURE OF ATOMS

To understand how atoms form molecules we must consider the structure of the atoms. No one, of course, has seen the interior of an atom, but modern physics gives us a picture of the atom which makes possible an explanation of how atoms interact to form molecules. According to this picture atoms are composed of extremely minute particles. Three kinds of particles will be considered in the following discussion, protons, electrons, and neutrons. All **protons** are alike and each one carries the same positive charge of electricity. All **electrons** are also alike, and each of them carries a negative charge of electricity equal but, of course, opposite to that on a proton. **Neutrons** are particles resembling protons but without an electric charge (Fig. 5:7).

An atom is pictured as consisting of a central portion called the **nucleus of the atom,**[1] containing protons and neutrons and an outer portion consisting of electrons only, arranged around the nucleus in **shells** or layers. The electrons are held in the atom by the attraction between their negative charges and the positive charges on the protons.

---

[1] The use of the term nucleus here for a portion of the atom is not to be confused with its use in the previous chapter for a part of the cell. The word is used in its original meaning of "kernel" or "central portion."

When the number of electrons in an atom is equal to the number of protons the total charge on the atom is zero and the atom is said to be a **neutral atom.** Certain atoms may gain or lose electrons. An atom in either of these conditions is said to be an **ion.** For the present we will confine our attention to neutral atoms. The atom of an element may be assigned a number which is equal to the number of protons in its nucleus. This is called its **atomic number.**[1] The atomic number of an element is also equal to the total (always positive) charge on the nucleus. The elements can then be arranged in a series according to their atomic numbers. The element of highest atomic number, uranium, has atomic number 92. Not all of the elements between hydrogen, atomic number 1, and uranium, atomic number 92, have been discovered but the gaps in the series are gradually being filled. It is possible that one or more elements with atomic numbers greater than 92 may be discovered or be artificially produced. This arrangement is very instructive since the physical and chemical behavior of an element seems to be dependent, ultimately, on the charge on its nucleus, which determines the number and arrangement of its electrons.

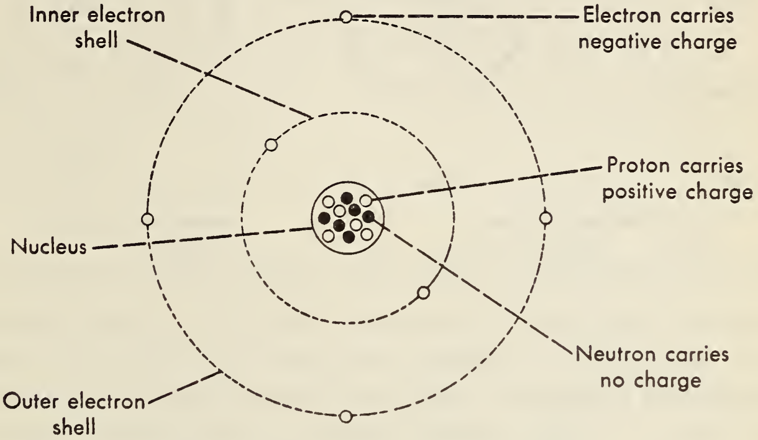

Inner electron shell
Electron carries negative charge
Proton carries positive charge
Nucleus
Neutron carries no charge
Outer electron shell

Fig. 5:7 Diagram to show features of atomic structure.

The **atomic weight** of an element (not to be confused with its atomic number) is not the actual weight in metric units of an atom of the element but the ratio of the weight of an atom of the element to the weight of an atom of hydrogen. Hydrogen having the lightest atoms, the weight of the hydrogen atom is taken as a unit.[2] The atomic weights of the lighter elements, which include most of those of biological interest, are approximately twice their atomic numbers.

---

[1] The atomic number of an element is not to be confused with its atomic weight, defined in the next paragraph.

[2] This is not entirely correct. The actual standard is oxygen taken as atomic weight 16. On this basis the atomic weight of hydrogen is 1.0078. However, for our purposes the difference can be ignored.

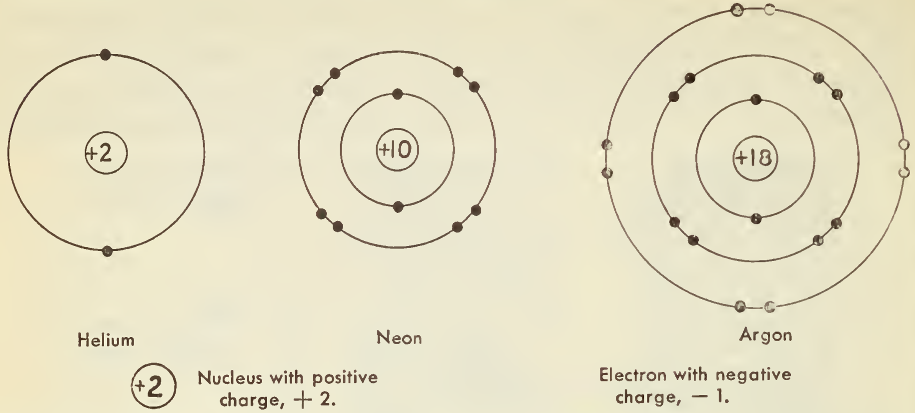

+2
+10
+18
Helium
Neon
Argon
+2
Nucleus with positive charge, + 2.
Electron with negative charge, — 1.

Fig. 5:8 Diagrams of atoms of helium, neon, and argon, showing electrons in shells.

As already indicated, the electrons occur in a series of concentric shells or layers about the nucleus as a center. Each shell may contain a certain number of electrons and as one passes from the elements of lower to the elements of higher atomic number and hence from elements with fewer to elements with more electrons the successive shells become filled with their quotas of electrons. The first or innermost shell is filled when it has two electrons. The second shell is filled when it has eight electrons. The third shell may have as many as eighteen electrons but before it

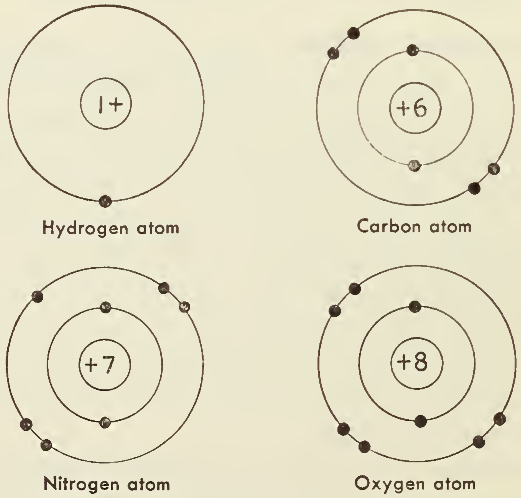
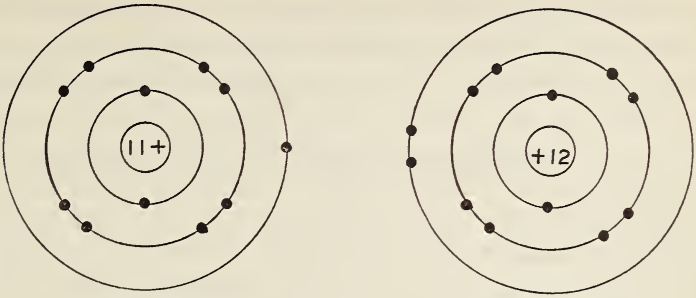
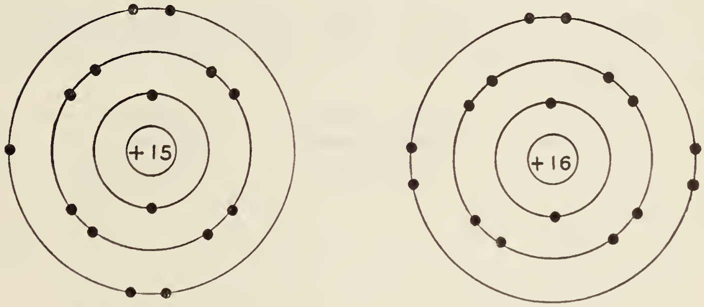


Fig. 5:9 Diagrams of atoms of hydrogen, carbon, nitrogen, and oxygen showing electrons in shells. These four elements make up ninety-nine percent of protoplasm. It will be noticed that they are all elements of low atomic number and of comparatively simple atomic structure.

becomes filled electrons begin going into the fourth shell. It will not be necessary for us to go beyond this point as the elements which occur in protoplasm are almost all elements of low atomic number.



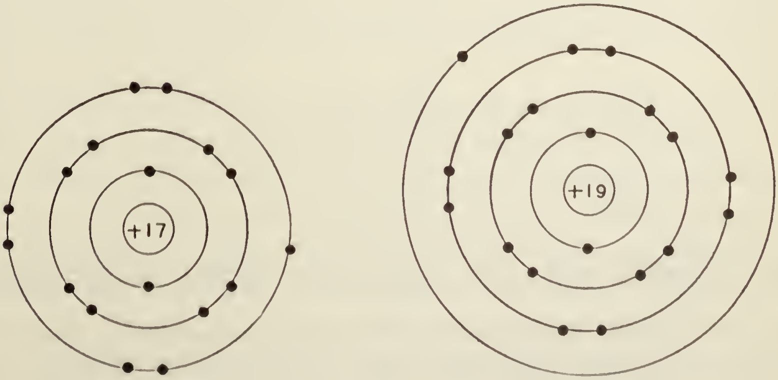
Sodium atom Magnesium atom



Phosphorus atom Sulphur atom

Fig. 5:10 Diagrams of atoms of sodium, magnesium, phosphorus, and sulphur showing electrons in shells.

The chemical behavior of an element seems to depend on the electrons in the outer shell of its atom. When this outer shell is filled the element is inert, i.e., it does not combine with any other element to form a com-



Chlorine atom Potassium atom

Fig. 5:11 Diagrams of atoms of chlorine and potassium showing electrons in shells.

pound. These **inert elements** form a series of rare gases found in the atmosphere (Fig. 5:8). The first is helium, atomic number 2, with its single electron shell filled by two electrons. The second is neon, atomic number 10, its first shell filled by two electrons and second shell filled by eight electrons. The third is argon, atomic number 18, in which the first shell has two electrons, the second eight, and the third eight.[1] We shall later find that the atoms of all elements, when the opportunity arises, tend to get a complete outer shell either by gaining, by losing or by sharing electrons. It is this tendency of atoms to complete their outer electron shells which gives rise to molecules and the formation of chemical compounds. The structure of the atoms of the elements which occur most commonly in protoplasm is summarized in the table (Table 5:5) and in diagrams (Figs. 5:9 to 5:11).

TABLE 5:5. THE STRUCTURE OF THE ATOMS MOST COMMONLY OCCURRING IN ORGANISMS AND THE INERT ELEMENTS HELIUM, NEON, AND ARGON

NAME OF ELEMENT	SYMBOL OF ATOM	ATOMIC NUMBER = POSITIVE CHARGE ON NUCLEUS	NUMBER OF ELECTRONS IN OUTER SHELL	NUMBER OF COVALENT BONDS
Hydrogen	H	1	1	1
Helium	He	2	2	—
—				
—				
—				
Carbon	C	6	4	4
Nitrogen	N	7	5	3
Oxygen	O	8	6	2
—				
Neon	Ne	10	8	—
Sodium	Na	11	1	1
Magnesium	Mg	12	2	2
—				
—				
Phosphorus	P	15	5	3
Sulphur	S	16	6	2
Chlorine	Cl	17	7	1
Argon	A	18	8	—
Potassium	K	19	1	1
Calcium	Ca	20	2	2

5. THE COMBINATION OF ATOMS TO FORM MOLECULES

The exact nature of the forces or other physical agents by which atoms are combined to form molecules is not clearly known. However, as already stated, the process is intimately dependent on the electrons in the outer shells of the atoms. Further, the electrons are involved in pairs, one member of the pair usually coming from one atom and the other member of the pair from the other atom. The term **valence bond**[1] is applied to the attractive or holding force which seems to act through a pair of electrons to unite two atoms.

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[1] In all of the elements above argon in atomic weight, except potassium and calcium, the third shell contains more than eight electrons, but this need not concern us here.

A. COVALENT AND COORDINATE BONDS

A molecule of **water** is composed of one atom of oxygen combined with two atoms of hydrogen (Fig. 5:12). This is indicated by the formula, H_2O, called the **molecular formula,** since it indicates the numbers of the different atoms combined in the molecule. It will be remembered that oxygen has the atomic number 8 and contains six electrons in its outer shell, i.e., its outer shell lacks two electrons of the stable number eight found in the inert gas neon. The atom of oxygen therefore tends to take on two electrons. The hydrogen atom has but one electron in its single shell and thus lacks one electron of the stable number in the corresponding inert gas helium which has two electrons. A stable condition

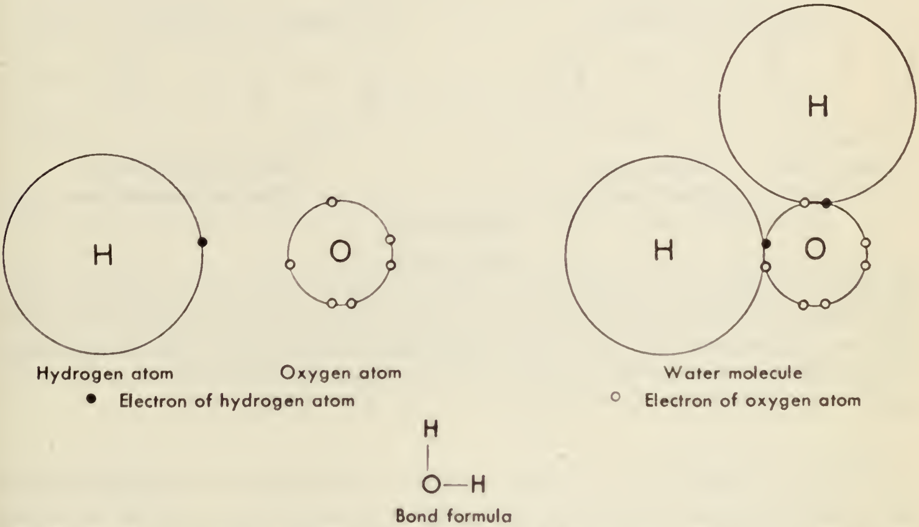

Fig. 5:12 Formation of a molecule of water by the sharing of electrons between the atoms of oxygen and hydrogen and the formation of covalent bonds. Only the electrons of the outer shells are shown.

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[1] "Valence" as a separate term has been avoided in this discussion since this approach is somewhat confusing to the beginner and it seems more enlightening to stress molecular structure and the role of the electrons. The valence of an atom may be defined as the number of atoms of hydrogen (or its equivalent) that will combine with, or be replaced by, the atom in question.

is arrived at by the atoms of oxygen and hydrogen when they combine to form water by the sharing of electrons. Each of the two hydrogen atoms shares its electron with the oxygen atom, thus this atom comes to have eight electrons in its outer shell, while the oxygen atom shares electrons with the hydrogen atoms, one to each, so that each of the hydrogen atoms then has two electrons, the stable number. When atoms are united by sharing electrons they are said to be joined by **covalent bonds** and the compounds are called **covalent compounds** (Fig. 5:12). Covalent bonds are usually indicated by short lines connecting the symbols for the atoms.

Another example of a compound in which the molecule is formed by electron sharing or covalence is **carbon dioxide,** CO_2. The carbon atom, it will be remembered, has four valence electrons and needs therefore four more to make its outer shell complete. Oxygen, on the other hand, has six valence electrons and requires two to complete its outer shell. The one carbon atom and the two oxygen atoms combine so that each of the two oxygen atoms shares two of its electrons with the carbon atom: in this way the outer shells of each of the atoms is made complete (Fig. 5:13). Covalent bonds occur in the formation of the molecules of elements. The common form of free oxygen consists of molecules each composed of two atoms. Each atom contains six outer electrons and therefore lacks two electrons of the stable number. Four electrons are shared, two from each atom, so that in the combined states the outer shells are completed.

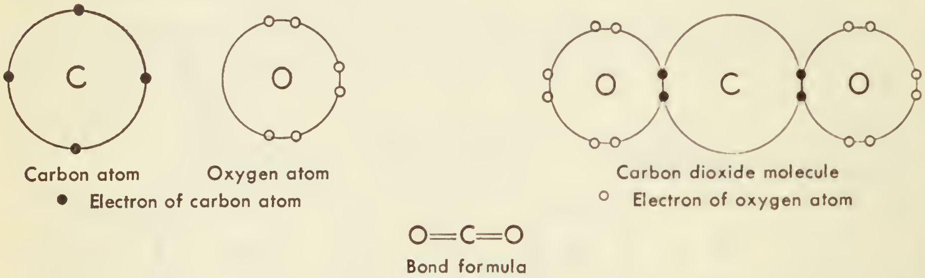

Fig. 5:13 Formation of a molecule of carbon dioxide by the sharing of electrons between the oxygen and carbon atoms. The carbon atom shares two of its four electrons with one oxygen atom and two with the other oxygen atom while each of the oxygen atoms shares two of its electrons with the carbon atom. The latter sharing is not represented in the diagram as it would then have to be in three dimensions.

A **coordinate bond** may be regarded as a special type of covalent bond in which the two shared electrons instead of coming originally one from each of the atoms, both come from one of the atoms. An example occurs in the case of the formation of an **ammonium ion.**[1] The gas ammonia, NH_3, is a compound in the molecule of which there are three covalent bonds which may be represented as in Fig. 5:14. Here the outer shell of each of the hydrogen atoms is completed by an electron shared with the nitrogen atom and the outer shell of the nitrogen is completed by electrons shared with the hydrogen atoms. In this arrangement there

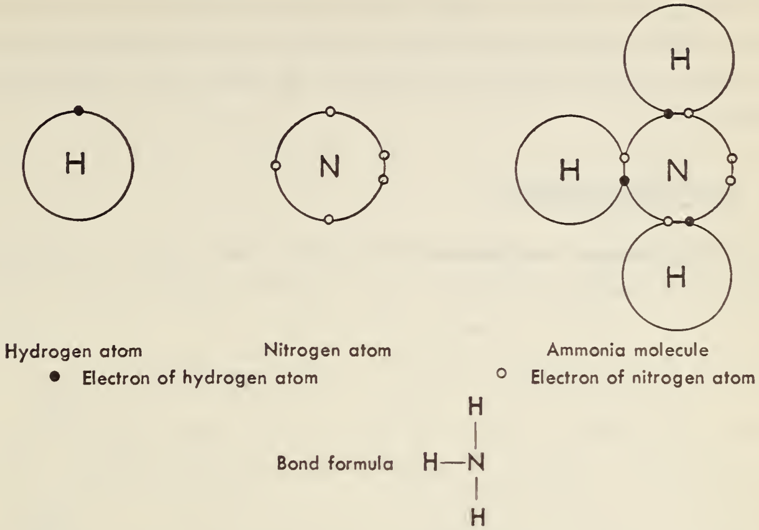

Fig. 5:14 Formation of the ammonia molecule by electron sharing in which there is left a lone pair of electrons in the nitrogen atom. The other electrons form covalent bonds.

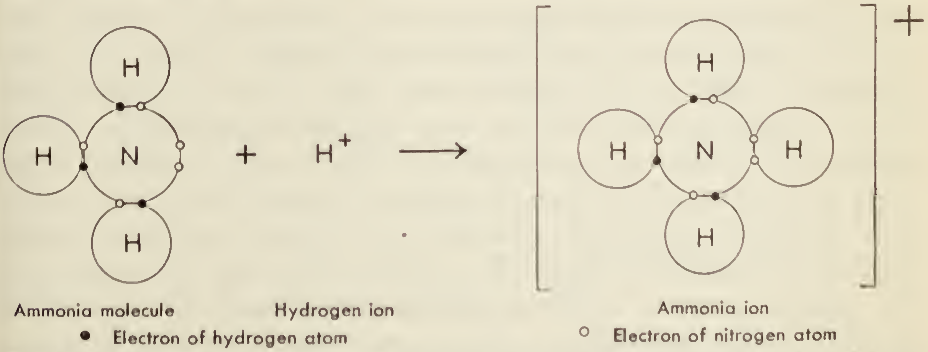

Fig. 5:15 Formation of a positive ammonium ion by electron sharing in which the lone pair of electrons of the nitrogen atom pick up a hydrogen nucleus. The bond formed in this case is a coordinate bond.

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[1] The formation of ions is considered in a later section (Section 7, C). An ion is formed from a neutral atom or a neutral molecule when one or more electrons are taken away from it or added to it. Since electrons carry negative charges when one or more of them are taken away from an atom or a molecule, the effect is that of giving the atom or molecule a positive charge. Conversely, when one or more electrons are added to an atom or molecule the effect is that of giving the atom or molecule a negative charge.

is a pair of electrons in the outer shell of the nitrogen atom which are not involved in the formation of any bond. These electrons are said to form a **lone pair of electrons.** When an ammonia ion is formed by the union of a hydrogen ion H^+ with a molecule of ammonia (Fig. 5:15) the lone pair forms the bond. Coordinate bonds differ from covalent bonds only in that both of the electrons of the shared pair come from only one of the atoms involved.

B. ELECTROVALENCE

In **electrovalent compounds** the molecules may be regarded as formed by the union of positive and negative ions, the ions being held together by the attraction which exists between oppositely charged bodies. An example is furnished by common table salt, **sodium chloride,** NaCl. The valence shell of the sodium atom contains one valence electron. The atom tends to lose this electron in order to attain the stable condition of eight electrons in the outer orbit. It then becomes a positively charged ion, Na^+. The atom of chlorine contains seven valence electrons. It therefore tends to take up an electron and become a negatively charged ion, Cl^-. When the positively charged sodium ion unites with the negatively charged chlorine ion a neutral substance, sodium chloride, is formed (Fig. 5:16). The bond which unites the sodium and the chlorine atoms is called an **electrovalent bond**. Compounds in which the atoms are united by electrovalent bonds are known as electrovalent compounds. Electrovalent compounds tend to dissociate into ions when in solution.

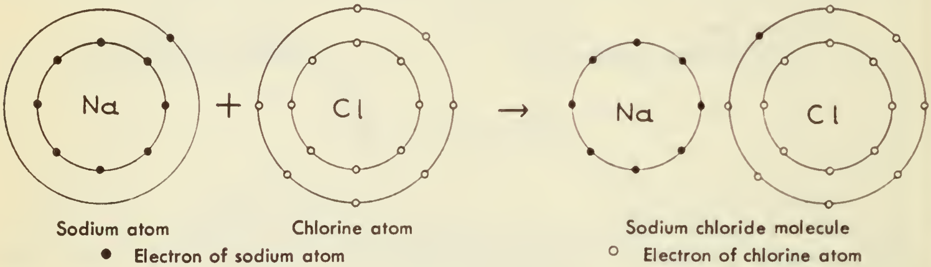
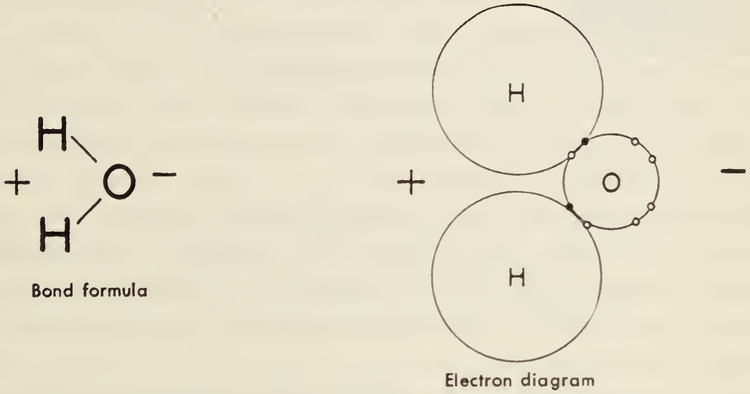


Fig. 5:16 Formation of sodium chloride. In this case an electron from the sodium atom passes to the chlorine atom forming an electrovalent bond.

6. POLAR AND NONPOLAR COMPOUNDS

The two types of union by bonds to form compound molecules discussed in the two previous sections indicate the existence of two types of compounds, already distinguished as covalent compounds and electrovalent compounds. Compounds may also be distinguished as nonpolar and polar compounds. The term **polar** is used to express the fact that the molecules of these substances, although neutral as a whole, nevertheless have electric charges distributed in them in such a way that one portion of the molecule is positive to another portion which is negative. In general, covalent compounds tend to be nonpolar, while electrovalent compounds are polar. However, many covalent compounds show a certain amount of polarity. Thus water, although its molecules consist of atoms united by covalent bonds, is a polar compound (Fig. 5:17). This polarity of the water molecule is explained as due to the shared electrons being held closer to the oxygen atom than to the hydrogen atoms and to the atoms being arranged to form a V rather than a straight line. Polar compounds are usually soluble in other polar compounds, e.g., sodium chloride in water; while nonpolar compounds are usually soluble in other nonpolar compounds, e.g., paraffin wax in benzene. On the other hand polar compounds are usually insoluble in nonpolar compounds, e.g., sodium chloride will not dissolve in benzene and, vice versa, nonpolar compounds are usually not soluble in polar compounds e.g., paraffin wax is not soluble in water.



Bond formula

Electron diagram

Fig. 5:17 A molecule of water to show polarity in a molecule.

7. SOLUTION

A. KINDS OF SOLUTIONS

When common salt, NaCl, is placed in water it dissolves and is said to go into solution. In this case the solution is one in which a solid, the salt, is dissolved in a liquid. A solution may also result when a gas such as carbon dioxide, CO_2, is dissolved in water as in ordinary soda water, or when another liquid such as alcohol is dissolved in water. In the above cases the water is called the **solvent** and the salt, carbon dioxide or alcohol,[1] the **solute.** In a solution, the substances become very finely divided so that the individual molecules (or ions) of the solute and solvent are uniformly dispersed among each other. A solution is not a compound since the proportion of solvent and solute may be varied. Neither is a solution a mixture since some of the properties, such as the boiling point and the freezing point, are different from those of the constituents. The **concentration of a solute** is the amount of the solute in a given volume of solvent, the volume usually taken being 1 liter or about 1 quart. A **dilute solution** or a solution of **low concentration** is one in which a relatively small amount of solute is present. A **strong solution** or a solution of **high concentration** is one in which the solute is present in large quantity. Substances differ in their **solubility,** i.e., their capacity to go into solution. When a given amount of solvent has dissolved all of a solute that it is capable of dissolving, it is said to be **saturated.** Some substances are practically insoluble, i.e., will not dissolve; others are slightly soluble; while still others are very soluble and may even dissolve in the solvent in almost any amount. The solubility of solid substances frequently increases with a rise in temperature. With gases it is usually the reverse, the solubility decreasing with increasing temperature. Since protoplasm contains a large amount of water (60 to 90 per cent) we are chiefly concerned with aqueous solutions or solutions in which water is the solvent.

B. DIFFUSION

In any solution the solute, if given time, becomes uniformly distributed in the solvent. This is due to diffusion. Diffusion can be easily demonstrated if a crystal of cupric sulphate ($CuSO_4 \cdot 5\,H_2O$), a blue salt of sulphuric acid, H_2SO_4, is placed in the bottom of a tall cylinder which is then carefully filled with water (Fig. 5:18). The cupric sulphate when it dissolves gives a blue color which is seen to extend gradually through the cylinder. The blue color is due to the cupric ions (Cu^{++}). If the water is kept undisturbed and at constant temperature, the blue color will rise slowly in the cylinder, indicating that the cupric ions are moving against the force of gravity and becoming distributed in the water. **Diffusion** may be defined as the movement of ions, molecules, or small aggregates of molecules from regions of high concentration to regions of low concentration. Under constant conditions, diffusion takes place very slowly and days may elapse before the solution in the above experiment gives a uniform blue color, showing that the cupric ions have become evenly distributed throughout the water. If the cylinder is shaken or the water is stirred, diffusion takes place much more rapidly. The rate of diffusion is also increased if the temperature is raised.

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[1] In the case of two liquids the one present in the greater amount is usually called the solvent. Thus in the case of alcohol over 50 per cent the alcohol would be referred to as the solvent and the water as the solute, but we will not ordinarily be concerned with such solutions.

Substances with small molecules or small ions,[1] and especially hydrogen ions, diffuse more rapidly than substances with large ions or large molecules which do not form ions, such as sugar. While diffusion in an undisturbed solution is slow when considered in terms of vessels of ordinary size, this is not the case in the microscopic dimensions of the cell. Thus an inorganic substance with relatively small molecules or ions may diffuse throughout a cell of average size in a few minutes.

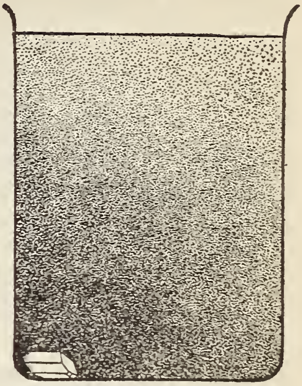

Fig. 5:18 Diagram of a colored substance dissolving and diffusing in water. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

C. ELECTROLYTES AND IONS

Based partly on their behavior in solutions, chemical substances may be divided into two groups called respectively **nonelectrolytes** and **electrolytes. Nonelectrolytes** when in solution occur as molecules dispersed among the molecules of the solvent. Such solutions are very poor conductors of the electric current. Chemical reactions between nonelectrolytes in solution usually take place slowly. Many of the substances found in organisms are classified as nonelectrolytes. For example, sugar and urea are nonelectrolytes. **Electrolytes** when dissolved in water break up into ions, a process called **ionization.** An **ion** is an atom or a group of atoms carrying one or more positive or one or more negative charges. Electrovalent compounds readily break up into ions when in solution. Thus sodium chloride, NaCl, yields sodium ions, Na^+, and chloride ions, Cl^-. However, covalent compounds may also act as electrolytes and yield ions by reacting with water. Thus when hydrochloric acid gas, HCl, is added to water, hydronium ions, H_3O^+, and chlorine ions, Cl^-, are formed (Fig. 5:19).

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[1] See Sec. C.

The case of water is somewhat peculiar. Two molecules react to form two ions. The nucleus of one of the hydrogen atoms of one of the water molecules breaks away, leaving its electron behind, and unites with the other water molecule. Thus from the two molecules of water two ions are formed, one of which is positive and contains in addition to the oxygen atom two hydrogen atoms and a hydrogen nucleus, while the other is negative and contains in addition to the oxygen atom one hydrogen atom and an extra electron (Fig. 5:20). The former ion,

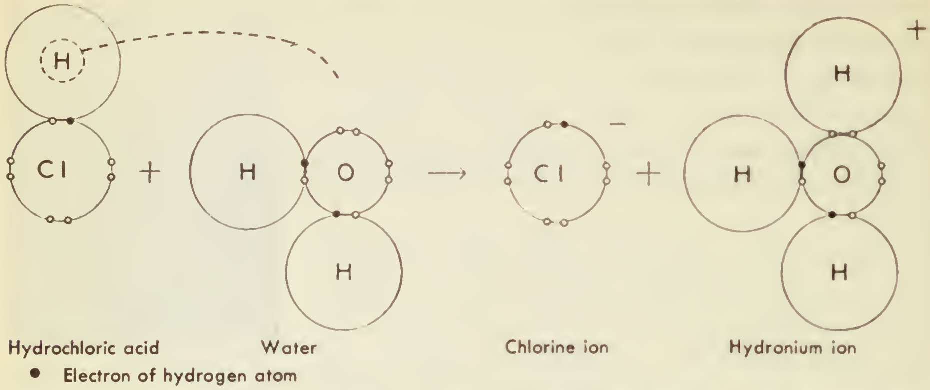

Fig. 5:19 Ionization of a covalent compound, hydrochloric acid. A hydrogen nucleus (a single proton) is transferred from the hydrogen atom in the hydrochloric acid to a water molecule.

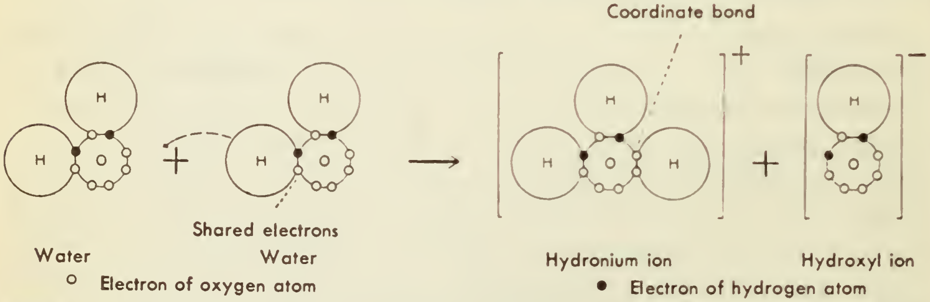

Fig. 5:20 Ionization of water. A hydrogen nucleus is transferred from one molecule of water to another molecule of water.

H_3O^+, is called the **hydronium ion,**[1] the latter ion, OH^-, is called the **hydroxyl ion.** The reaction goes on continually and in each direction, water molecules breaking up to form ions and ions recombining to form neutral water molecules.

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[1] According to the older chemistry the water molecule, H_2O, dissociated into hydrogen ions, H^+, and hydroxyl ions, OH^-. It is now believed that hydrogen ions seldom if ever exist alone in aqueous solutions.

A list of the ions commonly occurring in organisms is given in Table 5:6.

The distinction between nonelectrolytes and electrolytes is not a sharp one. Some substances ionize readily so that when they are in solution almost all of the substance is dissociated into ions, while other substances dissociate only slightly or almost not at all. Substances which dissociate readily into ions are called **strong electrolytes.** Solutions of such substances are good conductors of electricity because of the large number of ions present. Substances which dissociate only slightly into ions are called **weak electrolytes.** They are poor conductors of electricity. The ions of weak electrolytes combine readily with each other. This is why solutions of these substances tend to contain molecules rather than ions. The reverse is the case with strong electrolytes, their solutions containing ions rather than molecules because the ions do not combine. Sodium chloride is a strong electrolyte while carbonic acid is a weak electrolyte.

TABLE 5:6. IONS MOST COMMONLY FOUND IN ORGANISMS

POSITIVE IONS		NEGATIVE IONS	
Hydronium*	H_3O^+	Hydroxyl	OH^-
Ammonium	NH_4^+	Bicarbonate	HCO_3^-
Sodium	Na^+	Nitrate	NO_3^-
Magnesium	Mg^{++}	Nitrite	NO_2^-
Potassium	K^+	Dihydrogen phosphate	$H_2PO_4^-$
Calcium	Ca^{++}	Sulphate	SO_4^{--}
Iron	Fe^{++}, Fe^{+++}		

*See note p. 138.

Solutions of electrolytes are good conductors of electricity. Chemical reactions between electrolytes in solution occur rapidly. Substances classified as electrolytes include most acids, bases, and salts. They are discussed in a later section.

The **ionization of water** is of special interest because of its importance in biological systems. Water is an exceedingly weak electrolyte. In the case of pure water the number of hydronium ions, OH_3^+, is equal to the number of hydroxyl ions, OH^-. This is easily understood when it is remembered that each molecule of water which dissociates forms one of each kind of ion. The ionic concentration of pure water, i.e., the number of ions in a given quantity of water, is relatively small and constant.[1] The number is small because only a small proportion of the water molecules dissociate. The number is constant because, while the conditions remain the same, the rate of dissociation is equal to the rate of recombination.

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[1] Actually it varies somewhat with the temperature, but the variation within the limits of ordinary temperatures is slight.

When hydrochloric acid, HCl, is dissolved in water it dissociates into ions. When this occurs the hydrogen atom gives up its electron to the chlorine atom and unites with a molecule of water to form an hydronium ion, H_3O^+, while the chlorine atom after receiving the electron from the hydrogen atom becomes a chlorine ion, Cl^-. There is therefore an increase in the total number of hydronium ions in the solution or an increase in the **hydronium ion concentration.** We have already seen that when an hydronium ion encounters an hydroxyl ion a molecule of water is formed. As the number of hydronium ions is increased the number of encounters is increased. This leads to a decrease in the number of hydroxyl ions or a decrease in the hydroxyl ion concentration. Thus as the number of hydronium ions increases, the number of hydroxyl ions decreases. Careful experimental work has shown that the product, hydronium ion concentration multiplied by hydroxyl ion concentration, is a relatively constant quantity for all aqueous solutions (i.e., solutions with water as the solvent) under the same conditions.

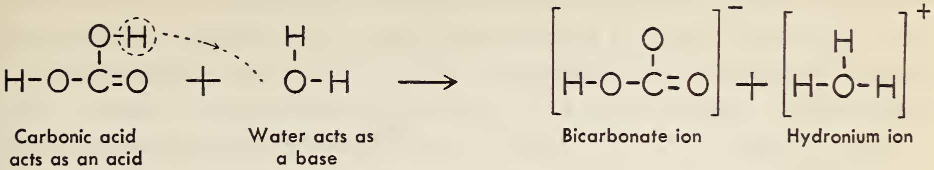
When sodium hydroxide is dissolved in water the ions formed are sodium ions, Na^+, and hydroxyl ions, OH^-. The addition of the hydroxyl ions to the solution leads to an increase in the total number of hydroxyl ions and, by reasoning similar to that pursued in the case of hydrochloric acid, the number of hydronium ions is in this case decreased.

8. ACIDS, BASES, AND SALTS

A. DEFINITIONS

When one thinks of an acid one is apt to have in mind acids like hydrochloric acid, sulphuric acid, or nitric acid which burn the skin and cause violent reactions when placed with many other substances. These are the acids commonly used in the chemical laboratory, mostly because they exhibit in a striking manner the properties of acids. But there are many other acids such as acetic acid which gives vinegar its sour taste, citric acid which occurs in oranges and lemons, and lactic acid which occurs in sour milk, which are less violent in their action. **Carbonic acid** is used in carbonated waters and gives them a bitter taste. Biologically, carbonic acid is one of the most important acids. When carbonic acid, H_2CO_3, is dissolved in water it dissociates to form hydronium ions, H_3O^+, and bicarbonate ions, HCO_3^-. A proton, H^+, (a hydrogen atom minus its electron) is transferred from the carbonic acid molecule to a water molecule which then becomes an hydronium ion, while the carbonic acid molecule becomes a bicarbonate ion (Fig.

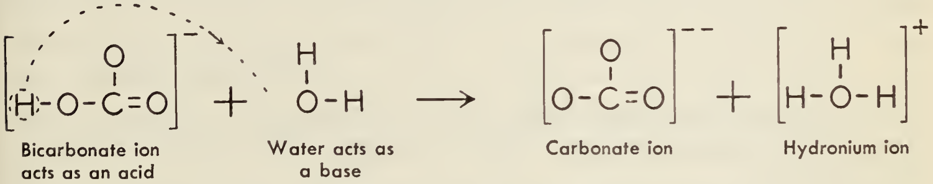
5:21). This reaction gives us the definition of an **acid.** An acid is a substance which can transfer protons to another substance.[1]



$$H_2CO_3 + H_2O \longrightarrow H_3O^+ + HCO_3^-$$

Fig. 5:21 The acid-base relations of carbonic acid. A hydrogen nucleus is transferred from the carbonic acid molecule to a water molecule. In this case water acts as a base.

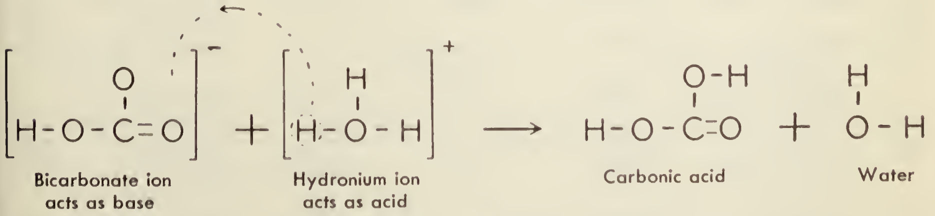
A **base** is a substance which can combine with one or more protons, i.e., it is a substance which can take up the protons given up by an acid. Thus in the first reaction (Fig. 5:21) the water molecule on the left acts as a base since it receives the proton given up by the carbonic acid molecule.



$$HCO_3^- + H_2O \longrightarrow H_3O^+ + CO_3^{--}$$

Fig. 5:22 The acid-base relations of the bicarbonate ion. A hydrogen nucleus is transferred from the bicarbonate ion to a water molecule. The resulting carbonate ion carries two negative charges.

The reaction between carbonic acid and water may go farther (Fig. 5:22). In this case the bicarbonate ion, HCO_3^-, acts as an acid,



$$HCO_3^- + H_3O^+ \longrightarrow H_2CO_3 + H_2O$$

Fig. 5:23 The reaction shown in Fig. 5:21 is here shown going in the reverse direction. In this case the hydronium ion acts as an acid giving up a hydrogen nucleus and the bicarbonate ion acts as a base receiving the hydrogen nucleus.

---

[1] This and the corresponding definition of a base are the newer definitions. The older definitions are not completely applicable to organic compounds nor to many biological phenomena.

giving up a proton to another water molecule, and becoming itself a carbonate ion, CO_3^{--}. Under certain conditions either of the reactions considered may go in the reverse direction (Fig. 5:23). In the first case the hydronium ion acts as an acid, giving up a proton to the bicarbonate ion which then behaves as a base. In the second case the hydronium ion behaves as an acid, and the carbonate ion as a base.

Thus on each side of the arrow in each of the reactions shown there is an acid which may give up a proton, and a base which may receive a proton. Also the base on the right, bicarbonate ion, HCO_3^-, in the first case, is the part of the molecule of carbonic acid, H_2CO_3, which is left after the transfer of the proton, H^+, to the water molecule. An acid and a base, which bear this relationship, such as H_2CO_3 and HCO_3^-, are called **conjugate acid and base** or corresponding acid and base. In the same reaction hydronium ion, H_3O^+, and water, H_2O, are also conjugate acid and base.

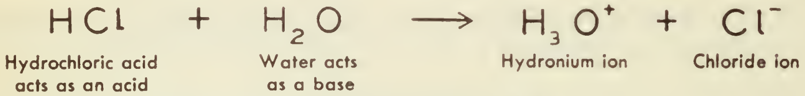

$HCl + H_2O \longrightarrow H_3O^+ + Cl^-$
Hydrochloric acid acts as an acid
Water acts as a base
Hydronium ion
Chloride ion

Fig. 5:24 Acid-base relations of hydrochloric acid.

Another example is provided by **hydrochloric acid,** HCl (Fig. 5:24). Here hydrochloric acid, HCl, and chlorine ion, Cl^-, are conjugate acid and base. Hydrochloric acid is regarded as a **strong acid.** The strength

TABLE 5:7. LIST OF CONJUGATE ACIDS AND BASES

	NAME OF ACID	FORMULA OF ACID	PER CENT DISSOCIATION IN 1/10 NORMAL SOLUTION[1]	FORMULA OF BASE	NAME OF BASE	
↑ Strong	Hydrochloric acid	HCl	92.	Cl^-	Chlorine ion	↑ Weak
	Nitric acid	HNO_3	92.	NO_3^-	Nitric ion	
	Sulphuric acid	H_2SO_4	61.	HSO_4^-	Hydrogen sulphate ion	
	Hydrogen sulphuric ion	HSO_4^-		SO_4^{--}	Sulphate ion	
	Phosphoric acid	H_3PO_4	27.	$H_2PO_4^-$	Dihydrogen phosphate ion	
Acid	Nitrous acid	HNO_2		NO_2^-	Nitrate ion	Base
	Carbonic acid	H_2CO_3	0.17	HCO_3^-	Hydrogen carbonate ion	
	Dihydrogen phosphate ion	$H_2PO_4^-$		HPO_4^{--}	Monohydrogen phosphate ion	
Weak	Bicarbonate ion	HCO_3^-		CO_3^{--}	Carbonate ion	Strong
	Monohydrogen phosphate ion	HPO_4^{--}		PO_4^{---}	Phosphate ion	
↓	Water	H_2O		OH^-	Hydroxyl ion	↓

[1] From *General College Chemistry*, by Joseph A. Babor and Alexander Lehrman, published by Thomas Y. Crowell, New York, 1940.

of an acid depends on the proportion of protons which are available in reactions with bases usually in solution in water. Hydrochloric acid is a strong acid because it is able to liberate large numbers of protons as indicated in the formation of large numbers of hydronium ions when it is dissolved in water. On the other hand, chlorine ion, which is the conjugate base of hydrochloric acid, is a **weak base.** It is a weaker base than hydroxyl ion and the hydronium ion goes to the hydroxyl ion in preference to the chlorine ion. Thus a strong acid has a weak conjugate base. The reverse is also true, that the conjugate base of a weak acid is a strong base. Or, in simpler words, the stronger the acid the weaker the conjugate base and vice versa. Water may be regarded as a very **weak acid,** the conjugate base of which is hydroxyl ion, OH^-, which is a very **strong base** (Fig. 5:20). The hydroxyl ion is a very strong base not because there are large numbers of hydroxyl ions formed but because the hydroxyl ion seems to have a great attraction for protons (Table 5:7).

B. NEUTRALIZATION

If a solution of hydrochloric acid, HCl, which is a strong acid, be mixed with a solution of sodium hydroxide which provides a strong base in the hydroxyl ion, OH^-, the resulting solution will be found not to contain large numbers of hydronium and hydroxyl ions. The law discussed in a previous section, that the product of the hydronium ion concentration and the hydroxyl ion concentration equals a constant quantity, still applies. Indeed, if the solutions were made up so as to contain exactly equal numbers of hydrochloric acid and sodium hydroxide molecules the mixture would be approximately neutral and contain approximately the same numbers of hydronium and hydroxyl ions as in pure water (Fig. 5:25). This occurs because the hydronium ions, H_3O^+, combine with the hydroxyl ions, OH^-, to form water, H_2O. In doing so they interchange charges and cease to be ions.

$$\underset{\text{Hydrochloric acid in solution}}{(H_3O^- + Cl^-)} + \underset{\text{Sodium chloride in solution}}{(Na^+ + OH^-)} \longrightarrow \underset{\text{Sodium ion}}{Na^+} + \underset{\text{Chlorine ion}}{Cl^-} + \underset{\text{Water}}{2H_2O}$$

Fig. 5:25 Neutralization of hydrochloric acid by sodium hydroxide. While the substances are in solution the sodium and the chlorine remain largely as ions and are not combined to form sodium chloride.

When the solution is evaporated and the water driven off the chlorine ions, Cl^-, from the hydrochloric acid unite with the sodium ions, Na^+, from the sodium hydroxide to form sodium chloride, NaCl. Sodium chloride is an example of a class of substances called salts. A **salt** is a substance which yields ions other than hydronium ions and hydroxyl ions. As in the example, salts are usually formed by the action of an acid on a base.

In this case, while the substances remain in solution the only permanent result of the reaction is the neutralization of the solution, i.e., the equalization of the numbers of hydronium and hydroxyl ions and the formation of water.

Hydronium ion concentration is exceedingly important in organisms. Most living processes can be carried on only in solutions relatively near to neutrality. If the protoplasm becomes either too acid or too basic, death ensues. As we will see in the following section special chemical mechanisms are employed to maintain constant the hydronium ion concentration of protoplasm.

C. *BUFFERS AND THE ADJUSTMENT OF THE ACID BASE RELATIONSHIPS*

As already stated, living processes require a rather delicate adjustment of the hydronium ion concentration. This is controlled in the living cell by the action of buffers. How this occurs may be best understood from an example. **Sodium acid carbonate**, or **sodium bicarbonate**, $NaHCO_3$, acts as a buffer in the blood and in protoplasm. This compound is the acid salt of a weak acid, carbonic acid, $H_2CO_3^-$. In solution $NaHCO_3$ becomes practically completely broken up into ions Na^+ and HCO_3^-.[1] The bicarbonate ion, HCO_3^-, may be regarded as a base. If now an acid stronger than carbonic acid such as hydrochloric acid, HCl, is added to the solution, the bicarbonate ions HCO_3^- are ready to receive its proton, H^+. Thus protons from the hydrochloric acid go to the bicarbonate ions rather than to the water molecules, so that carbonic acid, H_2CO_3, is formed rather than hydronium ions (Fig. 5:26). But

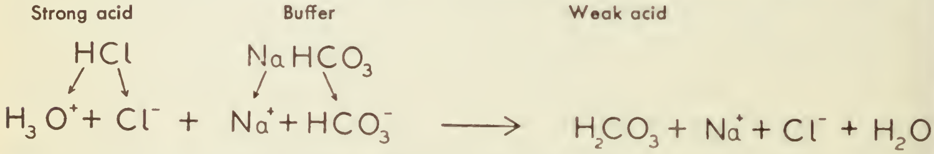


Fig. 5:26 Buffer reaction when a strong acid is added to a buffer in solution in water. The protons from the hydrochloric acid go to the bicarbonate ions rather than to the water molecules so that carbonic acid which is a weak acid is formed. Thus the acidity as measured by the hydronium ion concentration is not greatly increased.

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[1] A relatively small proportion of the bicarbonate ions HCO_3^- then dissociate, giving hydroxyl ions, OH^-, and carbon dioxide, CO_2, a gas which passes off.

carbonic acid is a relatively weak acid. Thus the acidity of the solution, even after the addition of the strong acid, HCl, is not much increased.

Suppose that instead of adding an acid to the sodium bicarbonate solution we add potassium hydroxide, KOH, which breaks up into potassium ions, K^+, and hydroxyl ions, OH^-, the latter of which acts as a strong base. In the presence of this strong base the bicarbonate ion, HCO_3^-, now acts as an acid. It gives up its proton, H^+, to the hydroxyl ions, HO^-, forming water molecules, H_2O. The strong base thus disappears and the solution is not greatly changed so far as its acidity is concerned (Fig. 5:27).

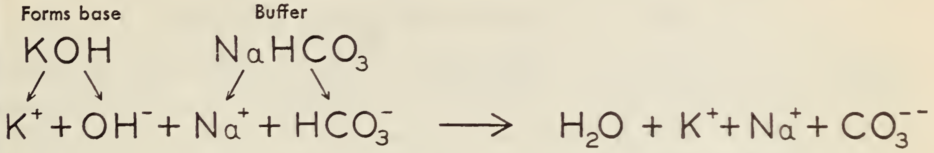

Fig. 5:27 Buffer reaction when a strong base is added to a buffer in solution in water. The bicarbonate ion gives up a proton to the hydroxyl ion and water is formed. Thus the alkalinity as measured by the hydroxyl ion concentration is not greatly increased.

A practical example may serve to illustrate further the action of buffers. A solution made by dissolving .01 gram (g) of hydrochloric acid in 1000 cubic centimeters (cu cm) of pure water is an exceedingly dilute solution. In fact it is about a .00001 per cent solution. Nevertheless, when 1 cubic centimeter of this solution is added to 1000 cubic centimeters of pure water the acidity of the solution measured by the hydronium ion concentration is 100 times that of pure water. Let us now add 1 cubic centimeter of this same .00001 per cent solution of hydrochloric acid to a solution made by heating beef in water. Such a solution contains buffers in the form of a small quantity of sodium bicarbonate and other organic substances (mainly proteins). When to 1000 cubic centimeters of such a solution, 1 cubic centimeter of the same hydrochloric acid solution is added, the change in hydrogen ion concentration can hardly be detected (Table 5:8).

TABLE 5:8. EFFECT OF ADDING ACID TO AN UNBUFFERED AND TO A BUFFERED SOLUTION

No buffer	
Pure water	1000 cu cm
Hydrochloric acid solution, .01 g per 1000 cu cm	1 cu cm
Hydrogen ion concentration is increased 100 times	
With buffers from beef	
Beef extract	1000 cu cm
Hydrochloric acid solution, .01 g per 1000 cu cm	1 cu cm
Hydrogen ion concentration practically unchanged	

9. ENERGY CHANGES IN CHEMICAL REACTIONS

In all chemical reactions energy is either stored or liberated. Thus when carbon combines with oxygen to form carbon dioxide as occurs when coal is burned, heat is given off. This may be expressed in a chemical equation:

$$\mathrm{C\ (solid) + O_2\ (gas) = CO_2\ (gas) + Energy}$$

Actually 8.1 kilocalories are given off per gram of carbon. It is necessary in such equations to specify whether the substances are solids, liquids, or gases, since to change from one of these states to another also requires energy. To separate the carbon atoms from the oxygen atoms there must be supplied an amount of energy equal to that which was given off when they combined. In this case the equation is simply reversed:

$$\mathrm{CO_2\ (gas) + Energy = C\ (solid) + O_2\ (gas)}$$

The amount of energy which must be supplied is 8.1 kilo-calories. Such a reaction occurs in green plants when the energy is supplied in the form of sunlight and becomes stored as chemical energy.[1] To take another example, when hydrogen and oxygen combine they do so with explosive force forming water:

$$\mathrm{2\ H_2\ (gas) + O_2\ (gas) = 2\ H_2O\ (liquid) + Energy}$$

The amount of energy in this case is 34.5 calories per gram of hydrogen or more than four times as much per gram as when carbon combines with oxygen. Carbon and hydrogen are utilized in animals and plants only in the form of compounds. The oxidation of such compounds provides the energy for their vital activities.

10. OXIDATION AND REDUCTION

The term **oxidation** was originally applied to the case where oxygen enters into combination to form a compound. Thus when coal is burned and oxygen combines with carbon, the process is called oxidation and the carbon is said to become oxidized.

$$\mathrm{C + O_2 \longrightarrow CO_2}$$

Oxidation

When the reverse occurs, i.e., when oxygen is taken out of a compound as occurs in plants when photosynthesis occurs, the process is called **reduction.** In photosynthesis only part of the oxygen is taken out of the carbon dioxide and hydrogen is added. The product of the reduction, $C_6H_{12}O_6$, is a simple sugar glucose.[1]

[1] See Chapter 16, Sec. 5, for a more detailed discussion.

$$6\,CO_2 + 6\,H_2O \longrightarrow C_6H_{12}O_6 + 6\,O_2$$

Reduction

It will be remembered that, in the case of CO_2, the oxygen atoms share electrons with the carbon atom. There seems reason to believe that when oxygen shares electrons with other elements the shared electrons are pulled toward the oxygen atom (Fig. 5:28). When the carbon becomes reduced the electrons of the outer shell of the carbon atom return to their normal place around the carbon atom. Because of this, oxidation and reduction have come to be regarded as essentially a movement of electrons, electrons being moved away from an atom when it becomes oxidized and toward it when it is reduced. This way of regarding the process makes it possible to extend the idea to cases where oxygen is not directly involved. When hydrogen combines with carbon to form the gas methane, CH_4, by sharing electrons, the electrons of the hydrogen

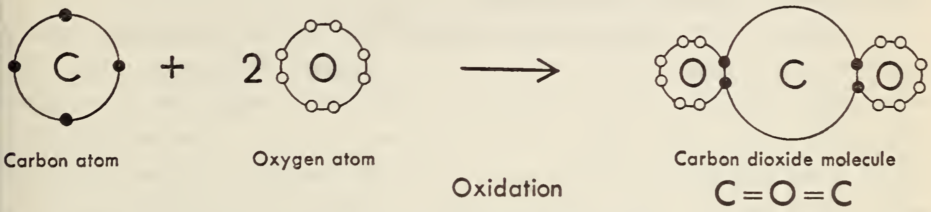

Fig. 5:28 Formation of a molecule of carbon dioxide from a carbon atom and two oxygen atoms to show oxidation. The electrons of the carbon atom are moved away from the nucleus of the atom. In this condition the carbon atom has the least potential chemical energy, i.e., it has given up all the energy it can.

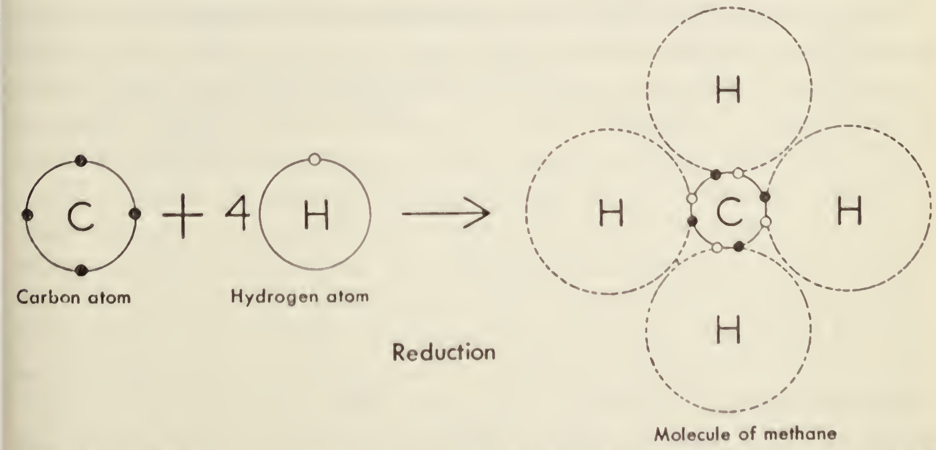

Fig. 5:29 Reduction of carbon by hydrogen to form methane. The electrons of the carbon atom are moved toward the nucleus. In this position the carbon atom has the greatest potential chemical energy, i.e., has the greatest store of chemical energy.

atoms move toward the carbon atoms (Fig. 5:29). Since the electrons move from the hydrogen atoms toward the carbon atoms the hydrogen is said to be oxidized and the carbon to be reduced. In fact, whenever carbon or any substance combines directly with hydrogen it is said to be reduced, and vice versa when any substance directly gives up hydrogen the substance is said to be oxidized.

It will have been noticed that the oxidation of one substance usually involves the simultaneous reduction of another substance and, vice versa, the reduction of one substance involves the oxidation of another substance at the same time. As will appear in detail later in discussing organic compounds, oxidation may occur in a series of steps. In a general way it may be said that an atom of a substance in the completely reduced condition contains a maximum amount of stored energy and that this energy is released as oxidation occurs, the energy stored becoming a minimum when oxidation is complete.

Oxidation and reduction are especially important in the chemistry of the cell because most of the energy changes which lead to vital activities involve oxidations and reductions. This will be better understood after the discussion of organic compounds in the next chapter.

11. CATALYSTS

A catalyst may be defined as a substance which increases the velocity of a chemical reaction without being used up in the process. An example is the action of platinum upon the combination of hydrogen and oxygen to form water. Ordinarily these two gases do not combine except so slowly that it is a matter of years before an appreciable amount of water is formed, unless an electric spark is passed through the mixture. However, if the gases are brought in contact with platinum, especially platinum in a very finely divided condition, the oxygen and hydrogen unite rapidly and may even explode. The explanation offered is that the oxygen and hydrogen atoms are held upon the surface of the platinum in such a way as to cause them to unite. The platinum is unchanged at the end of the reaction and can be used again. Different catalysts act in different ways and produce different effects. Hydrochloric acid may act as a catalyst by producing hydronium ions which act to hasten the reaction but do not appear in the final products. In a subsequent chapter there will be occasion to discuss the organic catalysts or enzymes which differ in a number of important ways from the inorganic catalysts referred to above.

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CHAPTER 6

Organic Compounds, Colloidal Systems, and Membranes

1. ORGANIC COMPOUNDS

A. SOME GENERAL CONSIDERATIONS

Apart from water, which acts chiefly as a solvent, the great bulk of the matter in living organisms consists of compounds of carbon with hydrogen, oxygen, nitrogen, and a few other elements. Such compounds are called **organic compounds.** Most vital activities are intimately dependent on the chemical activities of these compounds. Some knowledge of the nature of organic compounds and of their behavior is therefore essential to an understanding of the processes which go on in the bodies of plants and animals.

(1) SHARING ELECTRONS — GRAPHIC FORMULAS

The carbon atom, it well is remembered, has four of the eight electrons required for a complete valence shell of eight electrons such as occurs in the inert gas neon. The carbon atom does not gain or lose electrons and so far as at present known carbon never exists alone as a free positive or negative ion. In combining with other elements carbon always shares electrons.

In considering inorganic compounds not much attention was paid to the arrangement of the atoms in the molecules. This was because it is believed that in inorganic compounds usually only one arrangement of the atoms is possible. Hence in giving the composition of inorganic compounds only the numbers of each kind of atom in the molecule are given and the expression is called a **molecular formula.** Thus water is given as H_2O, sulphuric acid as H_2SO_4, and sodium phosphate as $NaHPO_4$. In organic compounds, however, not only are different arrangements possible but the different arrangements of the atoms represent different substances with different properties. Therefore it is usually not sufficient to indicate merely the numbers of the atoms in the molecule. The positions of the atoms in the molecules must be indicated and an organic substance cannot be completely defined until the arrangement of the atoms in its molecule is known.

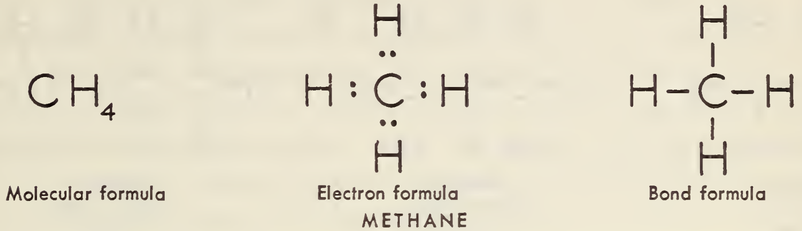


Fig. 6:1 Different types of formulas used in representing compounds in which only single bonds occur, illustrated by formulas for methane, marsh gas. The lines representing bonds each correspond to two electrons. The dots represent shared electrons.

The common method of showing the arrangement of the atoms in a molecule is to use a **graphic formula.** In organic compounds the atoms are held together in almost all cases by covalent bonds, which are formed by sharing electrons. Two types of graphic formulas are used, depending on the method employed to represent the bonds. In one type, which may be called the **electron formula,** the shared electrons are represented by dots, in the other type, called the **bond formula,** a pair of shared electrons is represented by one short line termed a **bond** (Fig. 6:1).

Each of these types of formulas as written on paper gives the impression that all of the atoms are in the same plane and that the plane is that of the paper. However, when there are more than three atoms in the compound this is probably seldom, if ever, the case. In methane the four hydrogen atoms are believed to be at the four corners of a tetrahedron (a figure with four equilateral triangular sides) with the carbon atom at the center (Fig. 6:2).

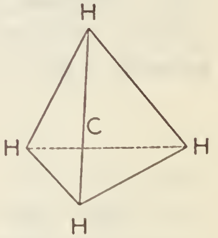
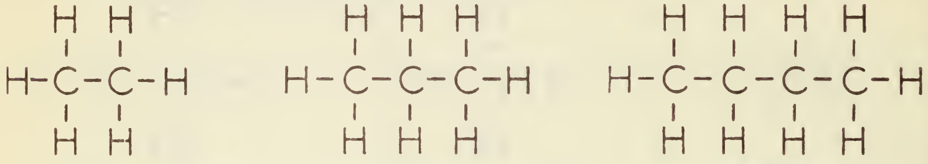


Fig. 6:2 Diagram of a methane molecule. The hydrogen atoms are at the four corners of a tetrahedron, a figure the sides of which are four equilateral triangles, and the carbon atom is in the center.

(2) THE LARGE MOLECULES OF ORGANIC COMPOUNDS

At the present time about 300,000 different compounds containing carbon are known. The existence of this vast number of compounds, many of them highly complex, is due to the unique ability of the carbon atom to share electrons with other carbon atoms. When joining together, the individual carbon atoms may bring with them the atoms of other elements. Thus long chains of groups of atoms in which each carbon atom acts as a kind of center are formed.

This capacity of carbon atoms to form chains is well shown in the series of compounds called **hydrocarbons,** so called because they are formed of carbon and hydrogen. **Methane,** CH_4, may be regarded as the first in a series of these compounds, others in the series being **ethane,** C_2H_6, **propane,** C_3H_8, **butane,** C_4H_{10} (Fig. 6:3). In the case of these compounds another type of formula may be used called the **structural formula** since it gives, like the graphic formula, the structure of the molecule. In this case the atoms connected with each carbon atom are grouped together. Thus butane may be written $CH_3(CH_2)_2CH_3$, indicating that at either end of the carbon chain is a carbon atom to which three hydrogen atoms are attached while the intermediate portion of the chain is formed by two carbon atoms to each of which two hydrogen atoms are attached. The carbon atoms which seem to form the axis of the molecules are called **carbon chains.** The carbon chains are not straight as might be concluded from the graphic formulas but are really zigzag in three dimensions. A carbon compound has been prepared in this series in which the carbon chain consists of seventy carbon atoms. The carbon chain may be branched. This is the case in the compound **isobutane** (Fig. 6:4).

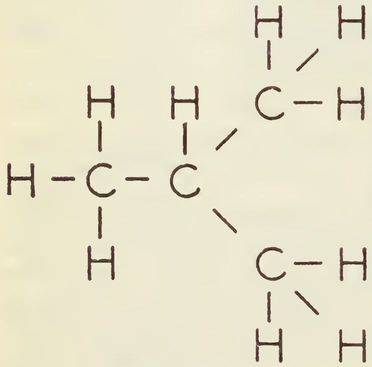


Ethane
CH_3CH_3
C_2H_6

Propane
$CH_3(CH_2)_1CH_3$
C_3H_8

Butane
$CH_3(CH_2)_2CH_3$
C_4H_{10}

Fig. 6:3 Three members of the hydrocarbon series with single bonds, ethane, propane, and butane.



Isobutane
$CH_3CH(CH_3)_2$ or C_4H_{10}

Fig. 6:4 Isobutane, a branched hydrocarbon with single bonds, which is also an isomere of butane.

Isobutane also illustrates another important feature of organic compounds. Isobutane, C_4H_{10}, has the same molecular formula as butane, but due to a different arrangement of the atoms in its molecule it is a different chemical substance with different properties. Two substances which have the same molecular formulas but in which the arrangement of the atoms is different are called **isomers.** Thus butane and isobutane are isomers.

The carbon compounds so far considered are called **open chain compounds** because, although the carbon chain may branch, the ends are not connected. In contrast to the open chain is the **ring** formation in which the carbon atoms are joined to form rings which in turn may be joined to form chains including rings. The single ring may contain from three to six carbon atoms but the commonest number is six. Examples of ring carbon compounds will be considered later.

Organic molecules vary in shape. Some are long and stringy, others are more compact, while many consist of more or less compact masses with long irregular masses extending out from them. Some idea of the size of an organic molecule can be obtained from the number of atoms which it contains. The molecule of hemoglobin, the red pigment in the blood, is believed to contain approximately 9000 atoms. The irregular shape of most organic molecules makes it difficult to assign them definite dimensions.

(3) DOUBLE AND TRIPLE BONDS

The carbon atom has been regarded as an atom with four outer electrons, thus needing four electrons to complete its outer shell and having four electrons to share. Graphically it has been pictured as extending four bonds out ready to attach itself to four other atoms. Actually there are atoms which require more than one bond. This is the case with the oxygen atom as is shown in **carbon dioxide** (Fig. 6:5). Here the oxygen atoms each share two electrons with the carbon atom, perhaps better expressed by saying that in place of one pair of electrons being shared two pairs are shared. This is represented in the graphic formula by a **double bond.** Thus a double bond indicates the sharing of two electrons by each of the atoms connected by the bond. The structure of a number of organic compounds is best explained by assuming that carbon atoms may be connected to each other by double bonds. A

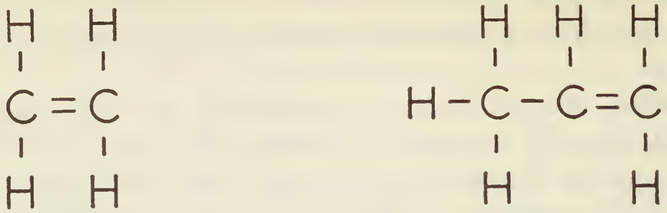
CO_2
Molecular formula

$O{:}{:}C{:}{:}O$
Electron formula

$O{=}C{=}O$
Bond formula

Fig. 6:5 Different types of formulas used in representing compounds in which double bonds occur, illustrated by formulas for carbon dioxide. The dots represent shared electrons. A double bond is represented by two lines and by four shared electrons.

double bond is indicated graphically by two short parallel lines. Simple cases of organic compounds containing a double bond connecting two carbon atoms are ethene, C_2H_4, and propene, C_3H_6 (Fig. 6:6). More rarely **triple bonds** occur as in ethyne, C_2H_2, and propyne, C_3H_4 (Fig. 6:7).

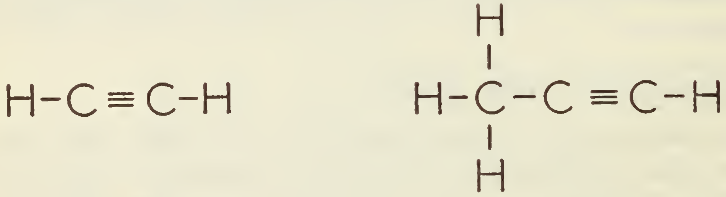


Ethene
$(CH_2)_2$ or C_2H_4

Propene
CH_3CHCH_2 or C_3H_6

Fig. 6:6 Two members of the hydrocarbon series with double bonds, ethene and propene.

It has been found that the union of two carbon atoms by a single bond is a rather stable combination, i.e., that it is one which does not readily separate in chemical reactions, while the double bond is much less stable. Thus organic molecules which contain double bonds in the carbon chain tend to separate into simpler compounds or combine with other atoms or molecules where the double bonds occur.



Ethyne
$(CH)_2$ or C_2H_2

Propyne
CH_3CCH or C_3H_4

Fig. 6:7 Two members of the hydrocarbon series with triple bonds, ethyne and propyne.

(4) THE ELEMENTS IN ORGANIC COMPOUNDS

The bulk of the molecule in most organic compounds is made up of carbon and hydrogen, usually with a certain proportion of oxygen. All proteins contain nitrogen also, but although nitrogen is an important constituent of these compounds the number of atoms of this element in a protein molecule is much less than the numbers of atoms of carbon or hydrogen. To these four elements must be added phosphorus and sulphur which occur in a number of protein compounds, and chlorine, bromine, and iodine which occur less frequently. As already stated, these elements are joined to the carbon atom by covalent bonds. These are listed with other information in Table 6:1.

TABLE 6:1. THE COVALENT BONDS OF THE ELEMENTS WHICH OCCUR IN THE MORE COMMON ORGANIC COMPOUNDS OF LIVING ORGANISMS

ATOMS		NUMBER OF COVALENT BONDS	ELECTRON FORMULA
Carbon	$-\overset{\vert}{\underset{\vert}{C}}-$	4	$\cdot\overset{\cdot}{\underset{\cdot}{C}}\cdot$
Hydrogen	$H-$	1	$H\cdot$
Oxygen	$-O-$	2	$\cdot\overset{\cdot\cdot}{\underset{\cdot\cdot}{O}}\cdot$
Nitrogen	$-\overset{\vert}{N}-$	3	$\cdot\overset{\cdot}{\underset{\cdot\cdot}{N}}\cdot$
Sulphur	$-S-$	2	$\cdot\overset{\cdot\cdot}{\underset{\cdot\cdot}{S}}\cdot$
Phosphorus	$-\overset{\vert}{P}-$	3	$\cdot\overset{\cdot}{\underset{\cdot\cdot}{P}}\cdot$

Note correspondence between number of single electrons and bonds.

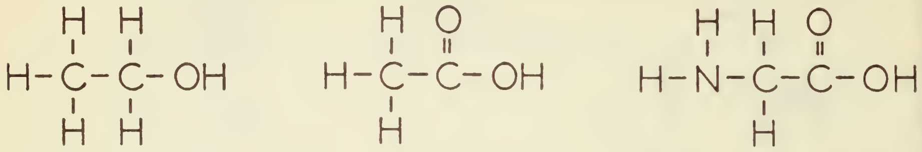
(5) FUNCTIONAL GROUPS

Hydrogen atoms attached directly to any of the carbon atoms in an organic compound can be replaced by other atoms or groups of atoms. The process is called **substitution,** the atoms or groups of atoms substituted are called **constituents,** and the substances formed by the substitution are called **derivatives.** It has been found that in many cases the chemical reactions of organic compounds depend more upon the substituted groups than on the hydrocarbon part of the molecule. For this reason such groups are called **functional groups.** Some of the functional

TABLE 6:2. THE FUNCTIONAL GROUPS WHICH OCCUR IN THE MORE COMMON ORGANIC COMPOUNDS OF LIVING ORGANISMS

FORMULA OF GROUP	NAME OF GROUP	SUBSTANCES FORMED
$-OH$	Hydroxyl	Alcohols
$-\overset{\overset{OH}{\vert}}{C}-O$	Carboxyl	Organic Acids
$-\overset{\overset{H}{\vert}}{N}-H$	Amino	Amino Acids

groups which occur frequently in organic compounds of biological interest are listed in Table 6:2. Any one of these groups may be substituted for a hydrogen atom attached to a carbon atom. In many cases, however, only one functional group is attached to one carbon atom.



Ethyl alcohol
CH_3CH_2OH or C_2H_6O

Acetic acid
CH_3COOH or $C_2H_4O_2$

Glycine
NH_2CH_2COOH or $C_2H_5NO_2$

Fig. 6:8 Compounds with different functional groups: ethyl alcohol, showing the hydroxyl group, —OH; acetic acid, showing the carboxyl group, $\overset{\overset{\displaystyle O}{|}}{C}\text{—OH}$; and glycine or amino acetic acid, showing the amino group $\text{H—}\overset{\overset{\displaystyle H}{|}}{N}$, and also the carboxyl group.

The following substances illustrate the occurrence of functional groups in organic compounds: ethyl alcohol (hydroxyl group), acetic acid (carboxyl group), glycine (amino group and carboxyl group) (Fig. 6:8).

(6) SOME GENERAL FEATURES OF ORGANIC COMPOUNDS

Some of the peculiar features which seem to stand out in the chemistry of carbon compounds may now be briefly summarized.

1. The carbon atom is known to unite with other carbon atoms and with the atoms of other elements only by sharing electrons. The substances formed in this way are frequently labile compounds, i.e., compounds which are easily changed chemically into other compounds. Many of the carbon compounds which occur in organisms are extremely labile.

2. Carbon atoms possess in a much higher degree than the atoms of any of the other elements the capacity to unite with each other while at the same time uniting with the atoms of other elements. This leads to the formation of a vast number of compounds with very large and complicated molecules. Further, these molecules when in water tend to become clumped together to form particles of submicroscopic size, a phenomenon which is referred to in the next chapter in the discussion of colloidal systems.

3. The elements which take part in the formation of carbon compounds are relatively few and, including carbon itself, are in general elements of relatively low atomic number. The complexity of organic molecules and their great variety arises from many different arrange-

ments and combinations of the atoms of these few elements. The complexity is not due to any great complexity in the atoms as such nor is it due to there being many different kinds of atoms involved.

B. THE ORGANIC COMPOUNDS IN PROTOPLASM

The list of known carbon compounds contains many substances which have been made in the laboratory but have not been found in organisms and quite probably do not occur in them. We will confine our attention to those substances which have been found in organisms and are known to play an important role in their metabolism. These substances include carbohydrates, fats and fatty substances, amino acids, proteins, vitamins, and hormones. This list does not include all the organic substances which occur in protoplasm as there are some substances which do not fit into any of these categories.

(1) CARBOHYDRATES

The term **carbohydrates** (L. *carbo*, charcoal + Gr. *hudor*, water) is used for a group of substances containing carbon, hydrogen, and oxygen, the hydrogen and oxygen being in the proportion to form water.[1] The carbohydrates of interest to the biologist may be classified into three groups, viz., monosaccharides (Gr. *monos*, one + *sakchar*, sugar), disaccharides (Gr. *di*, two), and polysaccharides (Gr. *polus*, many).

(a) MONOSACCHARIDES

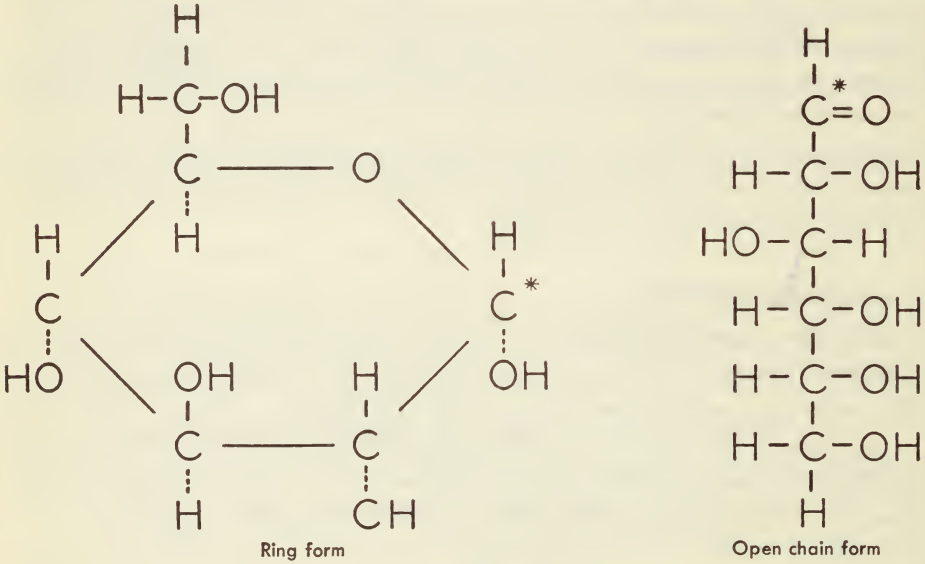
The most important of the monosaccharides are the hexoses, so named because they contain six atoms of carbon. The most important hexose from a biological point of view is **glucose,** called also **dextrose** and **cane sugar** (Fig. 6:9). The form shown is a ring compound with one short side chain. The ring is formed of five carbon atoms and one oxygen atom. Attached to each of four of the carbon atoms is a hydrogen atom and a hydroxyl group. The short side chain consists of a carbon atom with two hydrogen atoms and a hydroxyl group. The atoms and groups attached to the carbon atoms forming the ring are to be regarded as extending above and below the plane of the ring and not into the ring.

---

[1] This definition is not quite accurate as some sugars are known in which the proportion of hydrogen and oxygen is not that in water, and some other substances which are not regarded as carbohydrates contain hydrogen and oxygen in the proportion to form water, e.g., formaldehyde, CH_2O, and acetic acid, $C_2H_4O_2$. However, the definition above is approximately correct and will suffice for our present purposes. A better definition can be given in terms of the molecular structure.

Actually the atoms forming the ring are not all in one plane but form a zigzag somewhat similar to the zigzag in the case of an open chain of carbons. The molecule is to be regarded as containing two different kinds of functional groups, —OH and —O—.

There are several different forms of glucose depending on the relative positions of the H and OH groups. Also the ring of the glucose molecule may break and the ends separate to form an open carbon chain. The ring breaks between the oxygen atom in the ring and the carbon atom to the left of it in the graphic formula and this oxygen atom stays with the carbon atom marked with an asterisk, C* (Fig. 6:9). At the same time the OH group of the latter carbon atom, C*, goes to the carbon atom which lost the oxygen atom when the break occurred. The oxygen atom attached to the carbon atom, C*, seems to be mainly responsible for the peculiar properties of sugars and may be considered the primary functional group. Glucose is generally believed to be the sugar formed in the chloroplasts of plants in photosynthesis and it is the common form in which sugar occurs in the blood.



Glucose, $C_6H_{12}O_6$

Fig. 6:9 Glucose, a simple or hexose sugar. Both the ring form and the open chain form are shown. The ring breaks between the oxygen atom in the ring and the carbon atom marked with an asterisk.

Other hexose sugars with the same molecular formula as glucose, $C_6H_{12}O_6$, but differing from it in the arrangement of the H and OH groups are **mannose** and **galactose.** They are of interest chiefly as components of disaccharides and polysaccharides. **Fructose,** $C_6H_{12}O_6$, is another hexose sugar which enters into the composition of more complex sugars. In this case the ring contains four carbon atoms and one oxygen atom.

(b) DISACCHARIDES

One of the simplest of the disaccharides is maltose. **Maltose** is so named because it occurs in malt which is a mush made from the sprouted seeds of cereals. Malt is used in the manufacture of fermented liquors, the maltose being changed to alcohol, a process which will be referred to in a later chapter. Maltose is important in both animals and plants as one of the substances formed in the digestion of starch. The molecule of maltose may be regarded as formed by the combination of two molecules

$$\underset{\text{Glucose}}{C_6H_{12}O_6} + \underset{\text{Glucose}}{C_6H_{12}O_6} \longrightarrow \underset{\text{Maltose}}{C_{12}H_{22}O_{11}} + \underset{\text{Water}}{H_2O}$$

Fig. 6:10 The formation of a molecule of a disaccharide from two molecules of a monosaccharide, illustrated by the formation of a molecule of maltose from two molecules of glucose. This reaction is an example of condensation.

of glucose with the liberation of one molecule of water (Fig. 6:10). This type of process, which occurs frequently in organic reactions, is called **condensation.** When acted on by the enzyme **maltase** the maltose molecule breaks up into two molecules of glucose taking up one molecule of water. This process, which also occurs frequently in organic reactions, is called **hydrolysis** (Gr. *hudor*, water + *lusis*, a loosing).

The common sugar of the dinner table is **sucrose,** called also **saccharose** (not to be confused with saccharine). Hydrolysis of sucrose gives one molecule of glucose and one molecule of fructose. Its molecular formula is the same as that of maltose, $C_{12}H_{22}O_{11}$.

The principal sugar in the milk of mammals is **lactose.** It may be regarded as formed by the combination of one molecule of glucose and one molecule of galactose. When the enzyme **rennet** is added to milk to make "curds and whey" the fats and proteins are precipitated as the curds. The liquid portion remaining, which constitutes the whey, is mainly a solution of lactose.

It should be noted that when a sugar molecule is compared with a fat molecule, the sugar molecule contains a greater proportion of oxygen atoms. Thus glucose, $C_6H_{12}O_6$, contains the same number of oxygen atoms as carbon atoms and maltose, $C_{12}H_{12}O_{11}$, contains nearly as many. The sugar molecule is thus already partly oxidized and hence when it is oxidized to completion it yields less energy per carbon atom than the fat molecule. Actually one gram of sugar when oxidized to carbon dioxide and water yields approximately 4.1 kilocalories.

(c) *POLYSACCHARIDES*

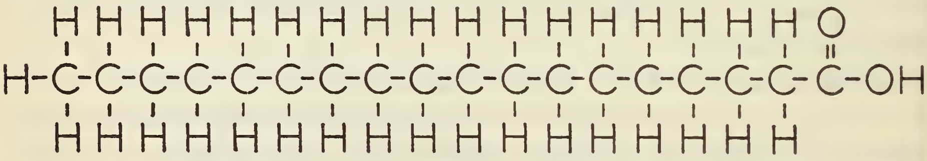
The molecule of a polysaccharide, like that of a disaccharide, may be regarded as formed by the combination or condensation of hexose molecules with the loss of water. The general formula for a polysaccharide is $(C_6H_{10}O_5)_n$, where n is usually a large even number.

The principal polysaccharides of biological interest are starch, glycogen, and cellulose. **Starch** is the common form in which carbohydrates are stored in the cells of plants. Being only slightly soluble, it is precipitated as small characteristic granules. The starches formed in different species of plants are different and are named after the species of plant. When the starch is required for food by the plant it is acted on by the enzyme **diastase,** and changed first to a **dextrin,** which is very similar to a starch, and then to maltose. Another enzyme, maltase, changes the maltose to glucose. Each of the steps is an hydrolysis. The process is called **digestion.**

The structure of a molecule of starch is not exactly known but it is believed to be composed of an even number of glucose molecules joined end to end. The molecular weights of starches are in the vicinity of 5000, which indicates that the molecule contains approximately 22 to 28 glucose units.

Glycogen, also known as animal starch, is similar to starch and like it hydrolyzes to glucose. Its molecule is somewhat smaller as indicated by a molecular weight of approximately 2000.

Cellulose is the main constituent of the walls of plant cells. Cotton is practically pure cellulose. Cellulose is insoluble in water and all organic solvents. It is closely related to the starches. When hydrolyzed it yields glucose, but the hydrolysis is much more difficult than in the case of starches. The molecule of cellulose is believed to be a long threadlike structure composed of many glucose units. The molecular weight of



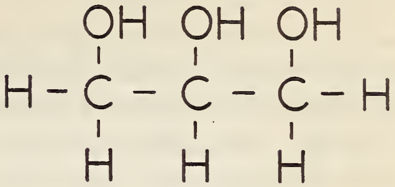
$$H-\underbrace{\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}-\overset{H}{\underset{H}{C}}}-\overset{O}{\overset{\|}{C}}-OH$$

Stearic acid

$CH_3(CH_2)_{16}COOH$ or $C_{18}H_{36}O_2$

Fig. 6:11 A molecule of stearic acid. Actually the carbon atoms are not in a straight line but form a zigzag in three dimensions.

20,000 to 40,000 indicates that there may be from 100 to 200 of these units. The units are believed to be arranged alternately, one side of the glucose ring being down in one unit and up in the adjacent units.



Glycerol

$CH_2OH \cdot CHOH \cdot CH_2OH$ or $C_3H_6O_3$

Fig. 6:12 A molecule of glycerol, which has three OH groups. The dots in the molecular formula are used to separate the groups attached to different carbon atoms.

(2) FATS

When digested in the body of an organism fats are broken down into organic acids called **fatty acids** and **glycerin** or **glycerol** and it seems likely that when they are synthesized in a cell it is by the combination of organic acids with glycerol. As already stated, organic acids are characterized by the carboxyl group $-\overset{\displaystyle O}{\overset{\|}{C}}-OH$. A common organic acid is **stearic acid,** $CH_3(CH_2)_{16}COOH$ (Fig. 6:11). Glycerol is an alcohol with the formula $CH_2OHCHOHCH_2OH$ (Fig. 6:12). The fat, **tristearin,** $C_{57}H_{110}O_6$, is formed when three molecules of stearic acid com-

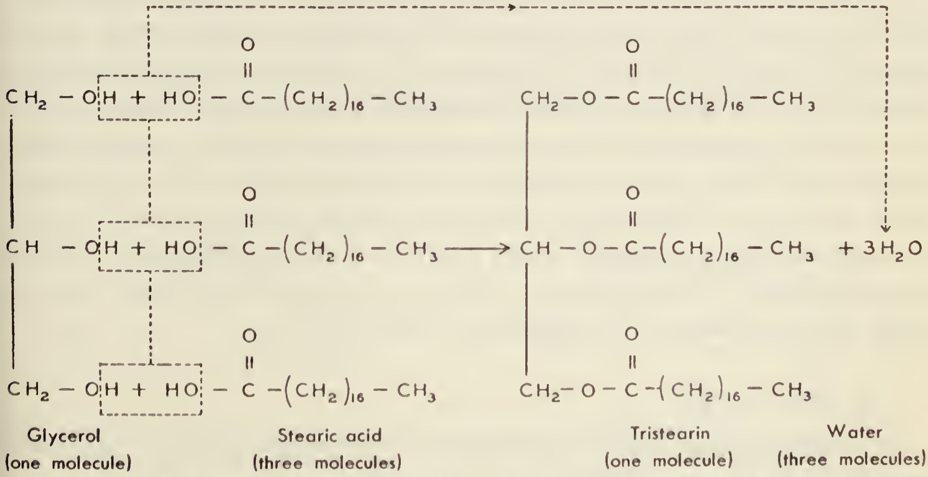


Fig. 6:13 The formation of a fat stearin (tristearin) from one molecule of glycerol and three molecules of stearic acid. The $H-\overset{H}{\underset{H}{C}}-$ group has been abbreviated to CH_3 and the $-\overset{H}{\underset{H}{C}}-$ group to CH_2.

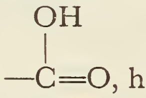
bine with one molecule of glycerol with the loss of three molecules of water. In the combination the carboxyl groups of the acid molecules unite with the hydroxyl groups of the glycerol (Fig. 6:13).

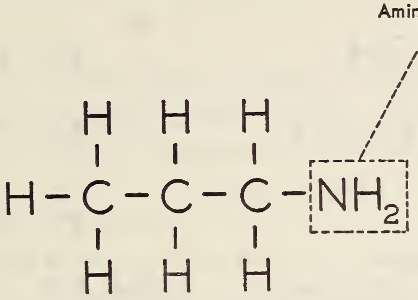
Two other important fats are **tripalmitin** and **triolein**. The molecule of tripalmitin is formed from one molecule of glycerol, $CH_2OHCHOHCH_2OH$, and three molecules of palmitic acid, $CH_3(CH_2)_{14}COOH$, with the loss of three molecules of water in the same way that tristearin is formed. This gives it a molecular formula of $C_{51}H_{98}O_6$. The molecule of triolein is formed from one molecule of glycerol and three molecules of oleic acid, $CH_3(CH_2)_7(CH)_2(CH_2)_7COOH$, with the loss of three molecules of water giving it the molecular formula $C_{57}H_{104}O_6$. These reactions are examples of condensation. These are the commonest fats in the bodies of mammals including man. There are, however, other fats formed from glycerol the molecules of which are formed from only two or even one fatty acid, the other OH group or OH groups of the glycerol molecule being unchanged.

The molecule of any one of these fats can be broken down into its constituent glycerol and fatty acid molecules. When this occurs one molecule of water is taken up by the glycerol part of the fat for each molecule of fatty acid formed. The process is an example of hydrolysis.

It should be noticed that in fats the proportion of oxygen in the molecule is small while the proportion of hydrogen is large. Thus in tristearin, $C_{57}H_{110}O_6$, of the 173 atoms in the molecule only 6 are oxygen while 110 of the atoms, or almost two-thirds, are hydrogen. Thus in a fat a very large proportion of the carbon atoms are completely reduced. This means that when a fat is oxidized to carbon dioxide, CO_2, and water, H_2O, as occurs in organisms a correspondingly large amount of energy is made available. Actually when 1 gram of fat is completely oxidized approximately 9.3 kilocalories of heat is liberated or enough heat to raise the temperature of 1 kilogram of water 9.3° C.

(3) AMINO ACIDS

A number of functional groups such as the alcohol group, —OH, and the carboxyl group,  $—\overset{\overset{\displaystyle OH}{|}}{C}{=}O$, have already been introduced in considering the molecular structure of carbon compounds. We now come to another functional group called the **amino group,** NH_2. An example of a substance containing this group is **amino propane** formed by replacing one of the hydrogen atoms of propane by an amino group (Fig. 6:14). **Amino acids** are mixed organic compounds in which the two functional groups are the amino group, NH_2, and the carboxyl or acid group, $\overset{\text{OH}}{\overset{|}{\text{C}}}\text{=O}$. The amino group is always found attached to the carbon atom next to that to which the carboxyl group is attached. The simplest of the amino acids is **glycine** or **amino acetic acid,** $C_2H_5NO_2$ (Fig. 6:15). Another important amino acid is amino proprionic acid (Fig. 6:16).

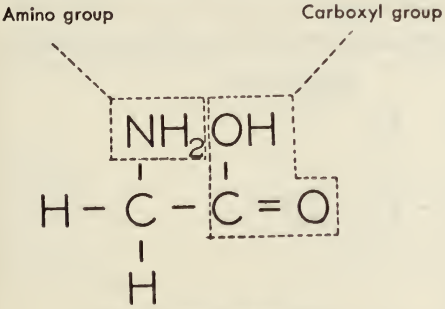


Amino propane

$CH_3 \cdot CH_2 \cdot CH_2NH_2$

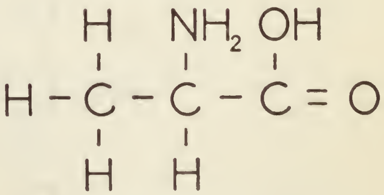
Fig. 6:14 Amino propane, an example of a substance in which a hydrogen atom is replaced by an amino group.

Amino acids are of interest to the biologist chiefly as the structural units from which the molecules of proteins are built. Some thirty-odd different amino acids have been isolated from the different animal and plant proteins so far investigated. Probably more will be found since several of these have been isolated only recently. Some amino acids have the form of chain compounds while others include one or more ring formations. There may be more than one carboxyl group and there may be more than one amino group. While the carboxyl group gives **acid properties** to the molecule, the amino group, which is related to



Glycine or amino acetic acid

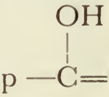
Fig. 6:15 Glycine or amino acetic acid, the simplest of the amino acids.

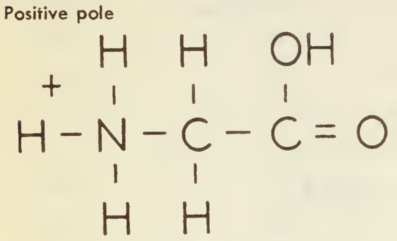


Amino proprionic acid

Fig. 6:16 Amino proprionic acid, a simple amino acid.

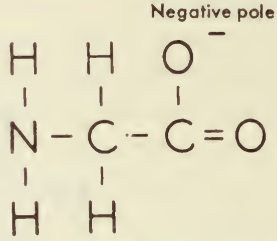
ammonia, NH_3, gives the molecule **basic properties.** Most amino acids are readily soluble in water.

When an amino acid is dissolved in an acid solution, i.e., one with an excess of hydronium ions, the amino group of the amino acid molecule takes up a hydrogen nucleus. This part of the amino acid molecule then comes to have a positive charge and the molecule becomes a **positive amino acid ion** (Fig. 6:17).[1] When, on the other hand, the amino acid is dissolved in an alkaline solution, i.e., one with an excess of hydroxyl ions (OH^-), the hydrogen atom of the carboxyl group  $—\overset{\text{OH}}{\overset{|}{C}}=O$ becomes a hydrogen nucleus and leaves the molecule to unite with a hydroxyl ion and form a molecule of water. When this occurs the acid part of the amino acid molecule is left with a negative charge and the molecule becomes a **negative amino acid ion** (Fig. 6:18). For most amino acids it is possible to find a hydrogen ion concentration near neutrality, at



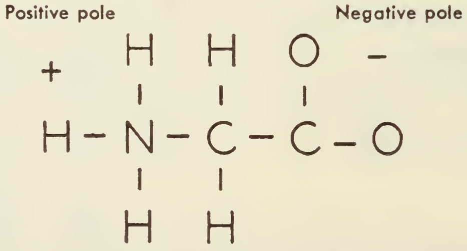
A positive glycine ion

Fig. 6:17 A positive glycine ion formed from a glycine molecule by the addition of a hydrogen nucleus, H^+, to the amino group. This gives the glycine ion a positive pole. Such ions occur in acid solutions.



A negative glycine ion

Fig. 6:18 A negative glycine ion formed by the loss of a hydrogen nucleus from the carboxyl group. This gives the glycine ion a negative pole. Such ions occur in alkaline solutions.



A polarized glycine molecule

Fig. 6:19 A polarized molecule of glycine formed by the addition of a hydrogen nucleus, H^+, to the amino group and the loss of a hydrogen nucleus from the carboxyl group. Such polarized molecules occur in neutral solutions.

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[1] Actually it is a little more complicated than indicated but the end result is as stated.

which one part of the molecule, that with the amino group, is positive while the other part, that with the carboxyl group, is negative. The molecule may then be said to be **polarized** (Fig. 6:19). Such polarized molecules readily join together, the positive part of one linking with the negative part of the other. This leads to our next topic.

(4) PROTEINS

The name "protein" comes from a Greek root meaning "to be first" and refers to the primary importance of these compounds for all living things. They are the principal nitrogen-containing substances in organisms. Our knowledge of proteins has come chiefly as a result of breaking them down into simpler substances. So far it has not been found possible to synthesize the more complex proteins in the laboratory. The composition of proteins varies somewhat but usually not greatly from the average given in Table 6:3. The protein molecule in most cases is exceedingly large and complex. As an example, the molecule of the red pigment in the blood may be taken. The molecule of this substance, called **hemoglobin,** is indicated by chemical analysis to be $C_{758}H_{1204}N_{195}S_3FeO_{218}$. This gives a molecule containing 2379 atoms with a molecular weight of 16,670. However, other measurements indicate that the molecular weight of hemoglobin is four times this amount, in which case both of the above figures would have to be multiplied by four. The molecular weight of one protein, **hemocyanin** (a pigment in invertebrates), has been determined by a physical method (ultracentrifuge) to be 5,000,000.

TABLE 6:3. PROPORTIONS BY WEIGHT IN WHICH THE CHEMICAL ELEMENTS OCCUR, ON THE AVERAGE, IN PROTEINS

	PER CENT WEIGHT	
Carbon	50	Occur in all proteins
Oxygen	25	
Nitrogen	16	
Hydrogen	7	
Sulphur	1 +	Occurs in most proteins
Phosphorus	1 −	Occurs in a few proteins

(a) HYDROLYSIS OF PROTEINS

The method usually used in studying proteins is to split the molecule into simpler substances by hydrolysis. In the **hydrolysis** of a compound the addition of a molecule of water causes it to divide into two substances one of which receives a hydrogen atom, H, from the water molecule while the other receives the OH group. The hydrolysis of proteins may be produced by a number of different methods which are effective in the following order: cold water, effective in only a few cases; boiling water;

superheated steam; dilute solutions of acids or alkalies; enzymes. As the hydrolysis of a protein proceeds, substances of gradually decreasing complexity arise and the process may be depicted as follows:

Protein ⟶ Proteoses ⟶ Peptones ⟶ Peptides ⟶ Amino acids

(b) DECOMPOSITION OF AMINO ACIDS

When the decomposition is carried further, the amino acids are **deaminized** giving rise to simpler organic acids and ammonia (Fig. 6:20); and **decarboxylized** (Fig. 6:21). In these processes foul odors are given off which are due to certain organic compounds occurring in the decomposition and to hydrogen sulphate when sulphur is present in the proteins. The end products include ammonia, NH_3, carbon dioxide, CO_2, and water, H_2O.

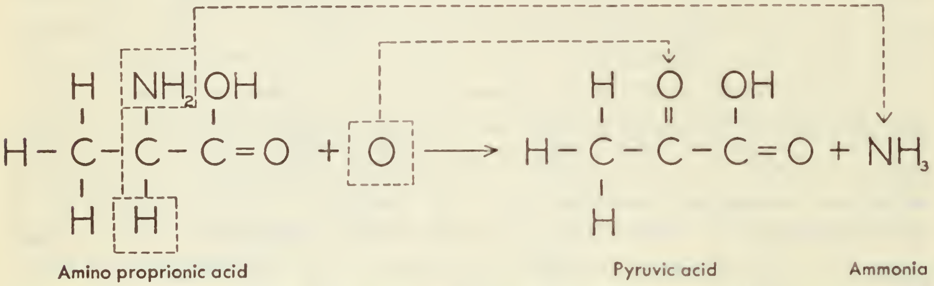

Fig. 6:20 Deaminization. In the example, the amino group and the hydrogen atom bound to the same carbon atom are split off as a separate ammonia molecule. The remaining part of the molecule becomes oxidized to pyruvic acid.

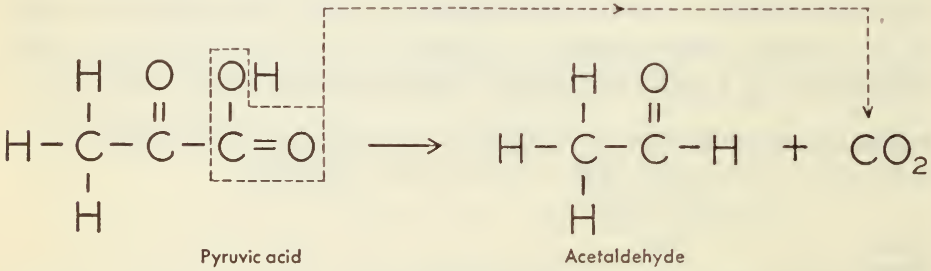

Fig. 6:21 Decarboxylization. In the example, the two oxygen atoms and the carbon atom of the carboxyl group are split off as a molecule of carbon dioxide, leaving a molecule of acetaldehyde.

(c) THE SYNTHESIS OF PEPTIDES

It would seem that any artificial synthesis of proteins would have to consist to some extent of a reversal of the steps taken in the hydrolysis. Amino acids have been combined to form peptides. A simple case is the formation of **glycyl-glycine** from two molecules of glycine (Fig. 6:22). The synthesis is formed by the union of a carboxyl group, $-\overset{\overset{\displaystyle O}{\|}}{C}-OH$, with an amino group, $-\overset{\overset{\displaystyle H}{\|}}{N}-H$, to form a junction of the form $-\overset{\overset{\displaystyle O}{\|}}{C}-\overset{\overset{\displaystyle H}{|}}{N}-$. During the process one molecule of water is liberated. This type of union is called **peptide linkage.** More complicated peptides have been made in the laboratory. The most complicated so far made was composed of eighteen amino acid molecules, fifteen of glycine, and three of another amino acid called leucine. This **polypeptide** had a molecular weight of 1213. In its general behavior it was similar to that of a natural peptone or proteose. It was even hydrolyzed by the enzyme trypsin. Since enzymes are highly specific in their action this is also evidence of its similarity to a natural peptone.

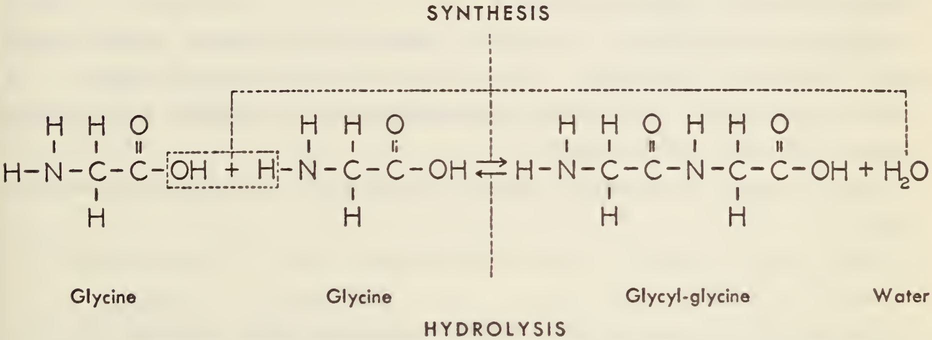

Fig. 6:22 Synthesis and hydrolysis of glycyl-glycine. In the synthesis, an oxygen atom and the associated hydrogen atom from a carboxyl group of one glycine molecule split off and unite with a hydrogen atom from the amino group of another glycine molecule to form a molecule of water, while the remaining parts of the glycine molecules unite to form a molecule of glycyl-glycine. In hydrolysis the process is reversed.

(d) KINDS OF PROTEINS

The number of different kinds of proteins is very large. Indeed the proteins of each plant or animal species seem to differ from those of other species, and some investigators have recognized differences in the proteins of individuals of the same species. That so many different kinds of proteins are possible is due to the large number of atoms in the protein molecule and the almost infinite number of combinations and permutations of these atoms which may occur. The following brief classification of proteins will give some idea of the extent of variation of proteins.

(5) A BRIEF CLASSIFICATION OF PROTEINS

Simple proteins. Proteins which yield only amino acids on hydrolysis. They include the following groups:

Albumins, including egg albumin, serum albumin of blood, and lactalbumin of milk.

Globulins, including serum globulin and fibrinogen of the blood, and proteins from the seeds of hemp and leguminous plants.

Prolamines, chiefly proteins from cereal grains.

Albuminoids, including keratin from hair, horns, and scales, and elastin and collagen from connective tissue fibers.

Histones from glandular tissue.

Conjugated proteins. Proteins which yield besides amino acids other nonprotein substances. They include the following groups:

Phosphoproteins, containing phosphorus and including casein from milk and vitellin from egg yolk.

Glycoproteins, containing carbohydrates and including mucin from saliva.

Nucleoproteins which make up the greater part of the proteins from the nuclei of cells.

Chromoproteins, containing pigments and including hemoglobin from the blood.

Lecithoproteins, containing lecithin, a fatty material and including thromboplastin which causes clotting of the blood.

Derived proteins. Proteins which do not occur naturally. They are proteins which have been formed either by the decomposition of naturally occurring proteins or by synthesis from amino acids. They include:

Primary derived proteins in which there has been no change from the original molecular weight or particle size. They include such proteins as fibrin formed from the fibrinogen of the blood, and egg white or coagulated albumin.

Secondary derived proteins are products of smaller molecular weight or particle size than the original protein. Included in them are proteoses, peptones, and peptides.

2. SURFACE ACTION

A **system** in the physicochemical sense is composed of masses of matter which interact. The masses of matter may be different substances or the same substance in different states. Each of these masses of matter which is homogeneous, i.e., the same throughout, and physically distinct from the others, is called a **phase.** For example, a piece of ice floating in water under an atmosphere of water vapor constitutes a physicochemical system in which there are three phases — ice, liquid water, and water vapor. These phases interact, for when the ice melts the amount of liquid is increased, and when evaporation occurs the amount of vapor is increased. The phases need not be different states of the same substance. They may consist of different substances and a single phase may contain more than one substance, provided the substances form a homogeneous mass as in the case of a solution.

The surface separating two phases, as the surface separating the ice and liquid water or the surface separating the water and the water vapor in the example given above, is called an **interface.** The interface between two phases is the scene of forces which affect the system or, as it is usually expressed, it is a region where energy becomes available to change the system. In biological systems this available energy shows itself chiefly in four forms: surface tension, concentration of substances in solution or in suspension at the interface, electrical charges on the interface, and a tendency for chemical changes to occur at the interface.

A. SURFACE TENSION

Almost everyone has seen the small insects known as "water striders" running over the surface of a pond or stream. Although heavier than water they do not sink below the surface. The same sort of thing occurs when a needle is made to float by gradually lowering it onto the surface of the water in a glass. In both cases the surface of the water acts as if it were a sheet of extremely thin rubber stretched over the water. The phenomenon is explained when the forces between the water molecules are considered (Fig. 6:23). The molecules of water are held in the liquid by the attractive forces between them. Below the surface these forces are equal in all directions. At the surface, however, a molecule is attracted only by the molecules below and on either side of it, the molecules of water in the water vapor over the liquid being too far away to exert any force on it.

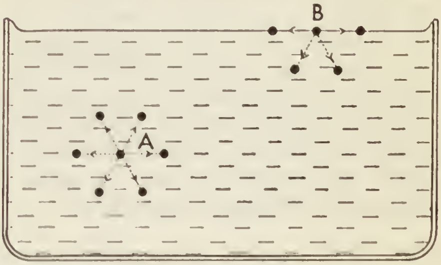

Fig. 6:23 Explanation of surface tension. The molecule A below the surface is attracted in all directions by the molecules surrounding it (six in the figure) while the molecule B at the surface is attracted only by the molecules at and below the surface. The resultant force on molecule B is therefore downward. Diagram from N. H. Black, *An Introductory Course in College Physics*, The Macmillan Company.

The molecules at the surface are therefore pulled downward or into the liquid and this tends to reduce the area of the surface when a reduction is possible or to oppose any increase in the area. This tension in the surface layer which tends to make its area a minimum is called **surface tension.**

Surface tension produces conspicuous effects when liquids occur in tubes of small diameter called **capillary tubes.** In this case, when a capillary tube is held vertically in a mass of liquid, there may be a difference in level between the liquid in the capillary tube and the liquid outside it (Fig. 6:24). When the attraction of the molecules of the liquid for each other is less than their attraction for the molecules of the walls of the tube, the liquid rises in the tube, as occurs when the liquid is water and the capillary tube is of glass. When the liquid is mercury and the capillary tube is glass, the level of the mercury in the tube is lower than the level of the mercury outside.

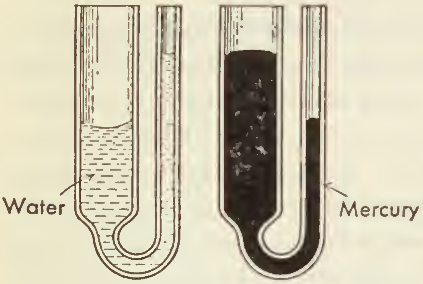

Fig. 6:24 Diagram to show capillary attraction and surface tension. The water in the capillary tube on the left rises above that in the larger tube, because the attraction of the water molecules for each other is less than the attraction of water molecules for glass molecules, and because relatively more molecules of water come in contact with the glass at the surface of the water in the capillary tube than in the larger tube. With mercury the reverse occurs, because the attraction of the mercury molecules for each other is greater than for glass molecules. Diagram from N. H. Black, *An Introductory Course in College Physics*, The Macmillan Company.

Surface tension is a factor in many vital phenomena. In the form of capillary attraction it is partly responsible for the rise of the sap in the minute vessels in the woody tissue of trees and other plants. It is also a factor in determining the shapes of cells, especially when they are without rigid cell walls. Thus many egg cells when suspended freely in a liquid medium assume a spherical shape, which is the form in which they present the smallest surface to the liquid.

Most substances when in solution lower the surface tension of the solvent, some much more than others. Fats and fatty substances are conspicuous in this respect, even a trace producing in some cases a marked effect. The effect of proteins may be considerable. Inorganic salts cause little change in the surface tension in the solvent. The **effect of substances in solution** on the surface tension is explained as due to the attraction between the molecules of the solute and the solvent being less than the attraction of the molecules of the solvent for each other. Thus when they are at the surface the force pulling the solute molecules down into the solution is less than the force pulling the molecules of the solvent into the solution.

Any substance which lowers the surface tension of a solution tends to become concentrated at the surface of the solution. This is explained in the same way that the effect of such substances on the surface tension is explained. When, due to molecular movement, a molecule of solute comes to the surface it tends to stay there and displace a molecule of the solvent because the force tending to pull it back into the solution is less than the force tending to pull a molecule of the solvent into the solution. This effect of surface tension in causing the accumulation of dissolved substances in the interface between two phases is of great importance in organisms as it appears to be one of the main factors in producing membranes such as the plasma membrane.

B. ADSORPTION

The concentration of the molecules of the solute at the surface of the solvent described in the preceding paragraph is called **adsorption.** Adsorption may be described as the concentration of the molecules of one substance at the surface of another substance.[1] Adsorption is of great importance in biological systems. The formation of colloidal particles is to be traced in part to adsorption.

C. ELECTRICAL CHARGES ON SURFACES

The particles adsorbed on a surface may be ions. In this case the surface becomes charged either positively or negatively. The same effect may result from the adsorption of polar substances at a surface when the polar molecules are oriented to the surface. As will appear later electrical charges are important in many biological systems. They are largely responsible for the maintenance of the particles of colloidal systems in suspension. Electrical charges on membranes may determine what will pass and what will not pass through them.

D. CHEMICAL ACTIVITY AT INTERFACES

Interfaces tend to be regions of chemical activity, i.e., regions where chemical compounds are formed or where they are broken up into their components. This is easily understood from the foregoing discussion of adsorption since chemical changes are apt to occur when different substances are brought into contact. Also the charge on the surface attracts ions of the opposite charge and these may enter into chemical combination. The catalytic action of certain surfaces referred to in the section on catalysts is an example of chemical action at an interface.

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[1] This statement does not distinguish between adsorption and absorption. The distinction is not always clear. Absorption is usually applied when one substance is included in another. Thus a gas may become absorbed into a liquid, which is practically equivalent to going into solution.

3. COLLOIDAL SYSTEMS

A. GENERAL DISCUSSION

If a glass of muddy water from a pond or marsh be set down and the contents allowed to settle, it will be noticed that the larger visible particles settle out first, then the smaller visible particles, after which the water may appear cloudy. If a portion of this cloudy water be examined under the microscope it will be found that the cloudiness is, in great part, due to particles too small to be visible to the unaided eye but visible under the microscope. In time the water, beginning at the top of the glass, will become clear, showing that the finer material, largely responsible for the cloudiness, is settling out. So far the particles have been of a size which made them visible at least under the ordinary microscope. The particles and the water are said to constitute a **dispersion system** — in this case, because the particles are visible, a coarse dispersion system. A dispersion system contains two phases; one phase, that represented by the particles, is called the **dispersed phase,** while

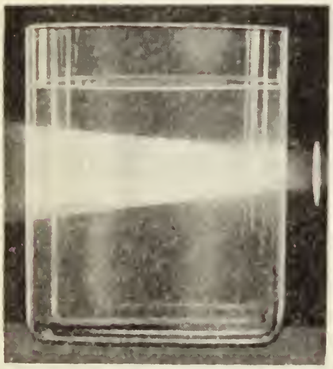

Fig. 6:25 Tyndall effect. The rays of light show as a bright region in the liquid. From McPherson, Henderson, Fernelius, and Mack, *Chemistry, A Textbook for Colleges*, Ginn and Company.

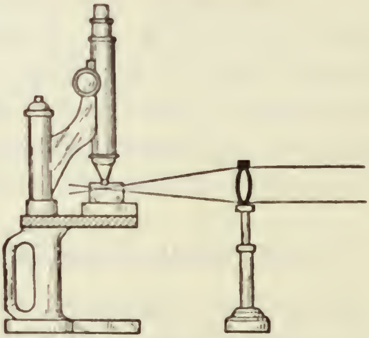

Fig. 6:26 The Ultramicroscope. The liquid, containing small particles, is illuminated at right angles to the direction of vision through the microscope. From Babor and Lehram, *General College Chemistry*, The Thomas Y. Crowell Company.

the other, represented in this case by the water, is called the **dispersing phase.**

If now a small beam of strong light is sent through the clear water in the glass at right angles to the line of sight, the part of the water illuminated will again appear cloudy to the naked eye. The optical effect obtained in this way is called the **Tyndall effect** (Fig. 6:25). When the same water is examined under the microscope and illuminated in the same way, i.e., by a strong beam of light parallel to the stage of the microscope, bright specks of light appear (Fig. 6:26). The presence of the bright specks of light is due to the fact that the particles, although too small to be seen under ordinary conditions, are, nevertheless, large enough to reflect light. This arrangement by which particles too small to be seen by ordinary methods are made visible as bright specks by reflected light is called the **ultramicroscope.**[1] It does not show the shape or outline of the particles. Particles such as those just described, which can be seen only with the ultramicroscope and are larger than ordinary molecules, are called **colloidal particles.** Together with the substance in which they are suspended, in this case water, they form a colloidal system. Colloidal particles pass through the pores of ordinary filter paper while the particles of a coarse suspension are held back. However, by using certain special types of filters, called **ultrafilters,** in which the pores are very fine, the colloidal particles can be caught and the water freed of them. After the dispersion system has been passed through a sufficiently fine ultrafilter only substances in solution remain in the water. It will be remembered that in a solution the individual molecules of the solute are dispersed among the molecules of the solvent.

As outlined above, the difference between a colloidal system and a coarse dispersion system on the one hand and a solution on the other hand depends on the size of the particles. The size at which a particle may be considered to be colloidal has been arbitrarily set at between 200 mμ and 1 mμ. Two hundred millimicrons is roughly the limit of size for visibility with the ordinary microscope and one millimicron is about the size of a fairly large molecule. Colloidal particles usually consist of many molecules. However, the very large molecules of some proteins may behave as colloidal particles. As seen in the ultramicroscope, colloidal particles are subject to a rather rapid **Brownian movement,** due to their bombardment by the molecules or ions of the dispersing phase (see page 122).

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[1] The ultramicroscope should not be confused with the ultraviolet microscope which, by using ultraviolet rays instead of ordinary visible light rays, is able to magnify objects slightly more than the ordinary microscope. Nor is it to be confused with the electron microscope which uses a beam of electrons to form the image and gives much higher magnifications. However, up to the present, the use of the latter has been limited to the magnification of very small objects maintained in a vacuum.

B. TYPES OF COLLOIDAL SYSTEMS

Various types of colloidal systems can be distinguished and they are classified in two different ways. One classification depends on the physical state of each of the phases, i.e., whether solid, liquid, or gas. Organic systems belong mainly to two of these types, viz., a liquid dispersed in a liquid, e.g., minute drops of oil in water, sometimes called an **emulsion,** and solid particles dispersed in a liquid, a form which protein systems frequently take. In cells the dispersing, or as it is often called, the **continuous phase,** is usually water and the dispersed, or **discontinuous phase,** may be a carbohydrate, a fat or fatty substance, or a protein. Colloidal systems may also be grouped according to the affinity existing between the dispersed and dispersing phases. When the substances of the two phases do not readily mix, as in the case of oil and water, the system is said to be lyophobic (Gr. *luein*, to dissolve + *phobos*, to fear). In such colloidal systems the Tyndall effect is pronounced and under the ultramicroscope the bright specks appear very bright and distinct. When the substances forming the two phases tend to mix, as is the case with starch and most protein particles, the Tyndall effect is much less pronounced and the specks of light under the ultramicroscope may be somewhat indistinct. This latter effect is interpreted as being due to the particles not having a sharp outline, owing to the adsorption of water molecules on the outer surface of the particles. Systems of this latter type are said to be lyophilic (Gr. *luein*, to dissolve + *philein*, to love). Lyophobic colloidal systems tend to be unstable, i.e., the particles tend to combine and settle out, while lyophilic systems tend to be stable.

C. THE LARGE INTERFACES OF COLLOIDAL SYSTEMS

For a given amount of dispersed substance, a colloidal system has a very large **interfacial area.** This is easily seen by comparing the surface area of the same amount of substance when contained in one mass and

TABLE 6:4. EFFECT OF REDUCING THE SIZE OF PARTICLES ON TOTAL SURFACE AREA

LENGTH OF SIDE OF CUBE	NUMBER OF CUBES IN TOTAL MASS	TOTAL SURFACE AREA
1 mm	1	6 sq mm
1 $\mu = 10^{-3}$ mm	10^9	6×10^3 sq mm
1 m$\mu = 10^{-6}$ mm	10^{18}	6×10^6 sq mm

when divided into particles. The shape or shapes of the particles makes a difference in the area but the calculation is easily made for a series of cubes (Table 6:4). It is seen that when a cube 1 millimeter on a side is divided into cubes 1μ on a side the surface area is increased one thousand times and that when the same cube is divided into cubes 1 $m\mu$ on a side the surface is increased one million times.

The large interfacial area which colloidal systems possess greatly increases the importance of the various types of surface action in determining the behavior of such systems. Thus, when dispersed in a colloidal system, a given quantity of substance can adsorb a vastly greater amount of another substance than when one compact mass. With this increased adsorptive capacity goes increased opportunity for chemical activity. Both of these processes figure prominently in the life of the cell. As will appear later it is difficult to imagine any form of life without a colloidal system. Indeed the presence of colloidal systems may be regarded as a major prerequisite for the appearance of living things.

The charges on colloidal particles are relatively large and when the charges are of the same sign the particles repel each other. This repulsion between the particles constitutes the chief factor in keeping the particles from settling out of the system in response to gravity.

D. SOLS AND GELS

When **gelatine,** which is a simple protein obtained from animal tissues, is added to hot water it appears to go into solution. Actually what is formed is a colloidal system, as can be shown by examining the liquid under the ultramicroscope or by ultrafiltration. If sufficient gelatine (10 to 12 per cent) was added and the system is cooled, the liquid will set into a jelly. The terms sol and gel are used to distinguish the two states of such a colloidal system. In the **sol** state the system behaves like a liquid. In the **gel** state it has certain of the features of a solid. If the gel in the above experiment is heated it becomes liquid again, i.e., the change from the sol to the gel state is in this case **reversible.**

Not all colloidal systems form gels similar to the one described. In many cases the material in the dispersed phase, instead of forming a jelly, coagulates to form a diffuse semi-solid mass called a **coagulum.** The change to a coagulum is not reversible. An example of this type of colloid is seen in the so-called white of the hen's "egg." This contains a simple protein called **albumin.** In an ordinary fresh egg the "white" is in the form of a clear liquid. When the egg is boiled this becomes an opaque white coagulum.

The structure of gels and coagula are of special interest as they suggest what may be the structure of protoplasm. It seems that the internal structure of a coagulum resembles a sponge with very fine pores. Gels, on the other hand, do not seem to be spongelike, but rather to consist of long fine fibers which pass through the liquid and support it.

4. MEMBRANES

A piece of filter paper is effective in keeping back or screening out the larger particles in a liquid because of its porous nature. In filter paper the pores are relatively large, as can easily be seen when a piece of such paper is examined under the microscope. Structures with much finer pores occur in nature and can be made artificially and are called **membranes.** Membranes can be made with pores of almost any size required to screen out the particles of a colloidal system. Thus substances in the dispersed phase can be separated from the system. Membranes which allow certain particles to pass and not others, whether on account of their size or their electrical condition, are called **differentially permeable** or **semipermeable membranes.**

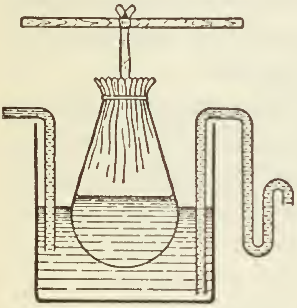

Fig. 6:27 A dialyzer. The liquid to be dialyzed is placed in a sack which is formed of a selectively permeable membrane. Substances which pass through the membrane pass out of the sack into the surrounding liquid which is changed by means of the system of tubes. From Babor and Lehrman, *General College Chemistry*, The Thomas Y. Crowell Company.

This principle is used in an apparatus called a **dialyzer,** used for separating impurities from colloidal systems. A membrane is made in the form of a bag or sack in which the colloidal system is placed. This sack containing the colloidal system is then placed in distilled water or some other suitable liquid. The dissolved substances and sufficiently small particles diffuse out through the pores of the sack into the surrounding water while the colloidal substance being dialyzed remains in the sack (Fig. 6:27). The liquid outside the sack is changed from time to time as the process proceeds.

When a membrane is formed from, or contains, a polar substance the molecules of the substance may become oriented so as to produce the effect of a charge on the surface, or ions may become adsorbed on the surface of the membrane and produce the same effect. When this is the case, ions in the solution with the same charge on them as the charge on the membrane are repelled from the membrane and do not pass through it, while ions with a charge of the opposite sign are attracted to the membrane and readily pass through. Thus the passage of particles through a membrane depends on other factors besides their size.

The pores of a membrane may be too small to allow the passage of the dissolved molecules or the ions of a substance through them, while allowing pure water or other dissolved substances to pass, or the membrane may be such that the molecules or ions of one substance pass through it only very slowly while those of another substance pass through it easily. Thus, for example, sugar molecules pass very slowly through a parchment membrane while pure water passes rapidly through such a membrane.

5. OSMOSIS

A differentially permeable membrane may give rise to a phenomenon called **osmosis** which is due to the difference in the rates at which different substances may pass through the membrane. How osmosis occurs can best be understood from an example (Fig. 6:28). Across the lower part of a U-tube is stretched a membrane which is permeable to water, but which allows cane sugar molecules to pass only very slowly. On one side of this membrane, the U-tube contains a 5 per cent solution of

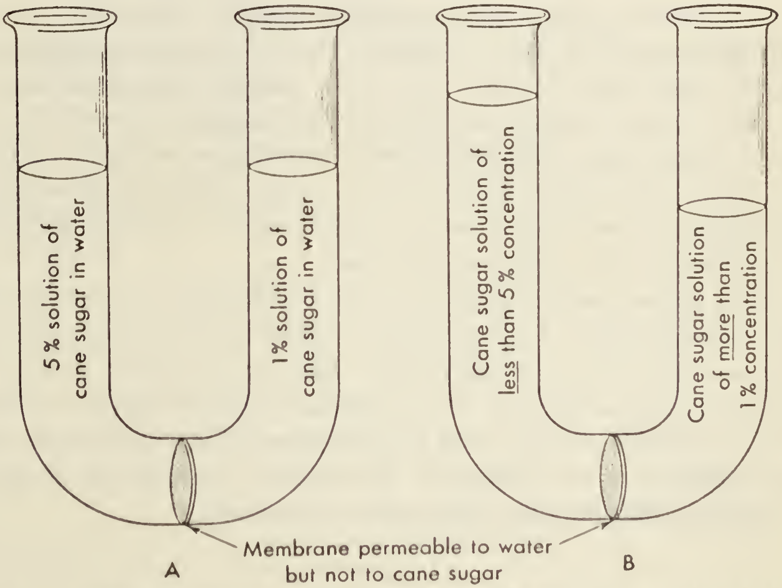
5% solution of cane sugar in water
1% solution of cane sugar in water
Cane sugar solution of less than 5% concentration
Cane sugar solution of more than 1% concentration
Membrane permeable to water but not to cane sugar
A
B

Fig. 6:28 Diagram illustrating diffusion through a differentially permeable membrane. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

cane sugar, and on the other side of the membrane, a 1 per cent solution of the same substance. If the amounts of the solution are so adjusted that they reach the same level in the two arms of the tube it will be found that after a time (Fig. 6:29 B) the level of the more concentrated solution (on the left) has become higher while that of the less concentrated (on the right) has become lower, and that the difference in level between the two solutions will continue to increase until a certain difference in level is reached, after which it will remain constant.

Since the cane sugar was unable to pass through the membrane this experiment shows that water passes through the membrane from the side where there is relatively more water to the side where there is relatively less water until a certain difference in pressure, represented by the difference in levels, exists on opposite sides of the membrane. This may be stated in another way which is more in conformity with our idea of diffusion. The water is more concentrated where the sugar is less concentrated, hence it moves from the side with the more dilute solution to the side with the more concentrated solution. The difference in pressure on opposite sides of a differentially permeable membrane due to solutions of different concentrations on the opposite sides of it is called **osmotic pressure.** The word "osmosis" is properly used to designate the passage of the liquid, in this case water, through the membrane, but its use has become ambiguous. Besides the changes in the levels of the solutions other changes have occurred; the volume of liquid on the left has increased while the volume of that on the right has decreased, the concentration of the solution on the left has decreased while the concentration of that on the right has increased.

In order for an osmotic pressure to be developed, it is only necessary for the concentration of the substance concerned in the process to be greater on one side of the membrane than on the other, and it is not necessary for the membrane to be absolutely impermeable to the substance; an osmotic pressure will be developed if the membrane merely retards diffusion of the substance. The plasma membranes of cells are very delicate, differentially permeable membranes.

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CHAPTER 7

Cell Physiology

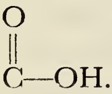
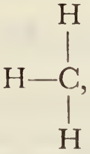
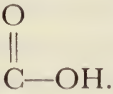
The importance of the cell as a structural unit in organisms has already been emphasized. The cell is equally important as a physiological unit. In the two preceding chapters the foundation has been laid for a consideration of the cell from this point of view.

1. THE PLASMA MEMBRANE

As already emphasized the plasma membrane must be clearly distinguished from the cell wall which usually surrounds the cell in plants, from the pellicle often found surrounding single-celled animals, from the cuticle frequently found on the outer surface of the epithelial cells covering plants and animals, and from the more extensive extra-protoplasmic structures found in bone, cartilage, and the skeletons of invertebrates. These are all formed outside the protoplasm as nonliving membranes and later become coagulated or precipitated to form the specific structures. The plasma membrane is also to be distinguished from differentiations within the cytoplasm, such as the ectoplasm of amoeba.

The discussions of surface action and membranes applied to inorganic systems in Chap. 6 may now be applied to the plasma membrane, which may be regarded as a differentially permeable membrane. By its permeability the plasma membrane determines what goes into and what comes out of the cell. Nevertheless it does not seem necessary to assume other than physical and chemical principles to explain its selectivity.

There is much evidence to show that the plasma membrane contains **proteins** and either fats or fattylike substances called **lipoids.** Evidence of the latter is found in two observations: first, cells exposed to a sufficient concentration of ether, which dissolves fats, disintegrate; second, substances which dissolve in fats readily enter cells. Proteins have been shown to be present in the plasma membrane of the red blood cell by the following method: As stated previously, the red cells burst when pure water is added to the blood plasma. When this is done the broken membranes can be separated from the protoplasm of the cells and the plasma of the blood by centrifuging and can then be submitted to direct chemical analysis for proteins.

Recently there has been developed a technique for studying the films which are formed when minute quantities of certain substances spread out on a water surface. If a minute quantity of a fatty acid such as stearic acid is added to pure water in a vessel, the stearic acid spreads out, forming a thin film on the water. If the amount of stearic acid added is not too great, the film will be only one molecule in thickness and is then called a **monomolecular film.** It will be remembered that the stearic acid molecule (Fig. 6:11) consists of a long chain of carbon atoms, with attached hydrogen atoms, and at one end a carboxyl group,  $\overset{\overset{O}{\|}}{C}\text{—}OH$. When the stearic acid molecules form a monomolecular film on the water the carboxyl group which is hydrophylic tends to hang down in the water, while the other end,  $H\text{—}\underset{\underset{H}{|}}{\overset{\overset{H}{|}}{C}}$, is on the outer surface, exhibiting hydrophobic properties. If not enough stearic acid has been added to make a film completely covering the surface, the molecules of stearic acid will lie out on the surface with their axes at an angle to the surface of the water. If, however, more stearic acid has been added, the molecules will be pressed together and placed so that their axes are perpendicular to the surface (Fig. 7:1). This monomolecular film, although it is only one molecule thick, has three definite regions, an outer region at the outer surface formed by the CH_3 ends of the molecule, an intermediate region consisting of the CH_2 part of the molecule, and an inner region formed by the carboxyl groups  $\overset{\overset{O}{\|}}{C}\text{—}OH$. In the outer region the ends of the molecules are forced together by the surface tension and form a smooth surface. The intermediate region containing the flexible chains of carbon atoms behaves somewhat like a liquid. In the inner region the carboxyl groups hang down into the water and are free to move parallel to its surface.

Monomolecular films can also be made with proteins, but the results are somewhat different. There is considerable evidence that the highly complex protein molecule, when in ordinary solution, has a globular form (approximately 250 to 300 mμ in diameter). When such molecules form a monomolecular film they become changed in shape so that they are only a third to a quarter as thick. Also when a protein such as egg albumin, which is soluble in water, is used to form a protein monomolecular film, the film behaves as if it were no longer soluble but rather a semisolid coagulum. The protein seems to be altered. The change is perhaps to be explained by assuming that hydrophobic groups in the protein molecule are buried in the interior in the ordinary soluble form but with the change in shape when the film is formed, these groups are brought to the surface of the molecule and the surface of the film.

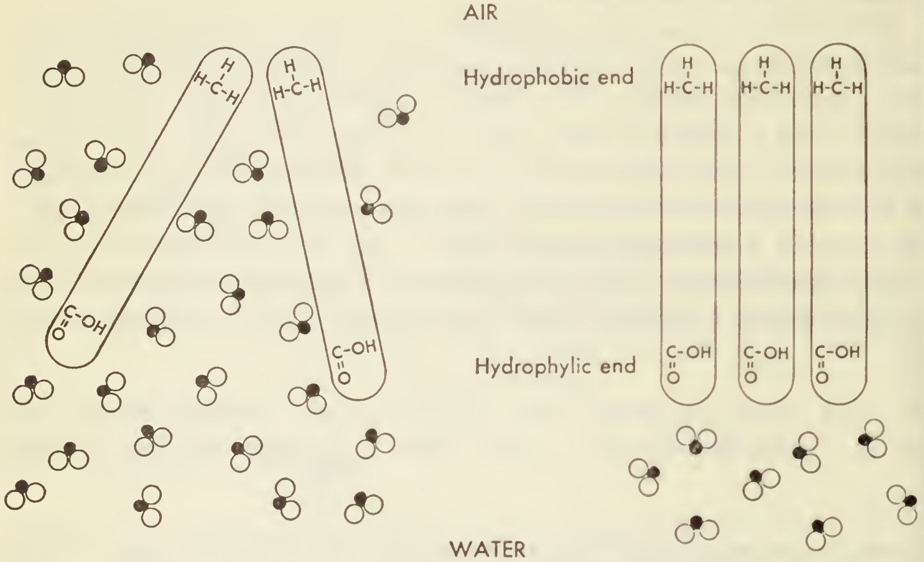


Fig. 7:1 Diagram to illustrate the structure of a monomolecular film. Such a film may be formed by dropping a very small quantity of stearic acid (see Fig. 6:11) on pure water. The molecules of stearic acid then tend to orient themselves so that the carboxyl ends $\overset{\text{O}}{\overset{\|}{\text{C}}}\text{—HO}$ are down in the water while the other ends are at the surface. When there is not enough stearic acid present to make a compact film the molecules may be somewhat irregularly oriented. When more stearic acid, but not enough to make a double film, is present the molecules arrange themselves at right angles to the surface and parallel to each other.

Water passes easily through the plasma membrane. Gases such as oxygen and carbon dioxide do not pass through the plasma membrane as pure gases but readily pass through it in solution in water by diffusion. In general, neutral molecules pass more readily than charged ions, and of the latter, positive ions such as those of potassium (K^+) and sodium

(Na$^+$) pass more rapidly than negative ions such as the chlorine ion (Cl$^-$) or the bicarbonate ions ($KHCO_3^-$, $NaHCO_3^-$). Weak acids which dissociate only slightly consist mostly of neutral molecules and like them readily penetrate the membrane. Fat-soluble substances have already been mentioned as passing rapidly through the plasma membrane. Molecular size would seem to be of secondary importance up to a certain point, but the large molecules of polysaccharides, fats, and proteins, at least in most cases, seem to be unable to pass through.

The observations seem to be explained if the membrane is a mixture of fat and protein molecules arranged in the form of a mosaic, fat and protein molecules alternating, and the protein molecules carrying negative charges of electricity. The fat-soluble materials pass through the regions bounded by fat molecules. The other undissociated molecules and the positive ions pass through the spaces between the protein molecules. Negative ions are repelled by the negatively charged protein molecules. The molecules of polysaccharides, fats, and proteins are unable to pass between the protein molecules because of their size.

2. THE FINER STRUCTURE OF PROTOPLASM

Since protoplasm may properly be called the physical basis of life there is great interest in its finer structure — in the arrangement of the molecules and groups of molecules of which it is composed. For in this finer structure quite as much as in its chemical composition must be sought the explanation of its many and various activities. The problem may be approached from two quite different points of view.

By using the various methods of obtaining **magnified images** of small objects such as the highest powers of the ordinary compound microscope, the ultraviolet microscope, and the electron microscope, together with data to be obtained with X rays, the attempt may be made to obtain a graphic representation of the structure.

Many difficulties are encountered in trying to obtain by optical methods a clear representation in three dimensions of the finer structure of protoplasm. One such difficulty arises from the fact that the cytoplasm is continually changing so that its appearance and presumably to some extent the arrangement of the materials of which it is composed vary with the conditions under which it is observed. Hence observations on dead protoplasm are of very questionable value. A second difficulty is due to the fact that with the techniques named, the structure is viewed from one point and in one plane only, at any one time. As a result of these difficulties there has been disagreement as to the interpretation of the observations, and a number of different theories of the structure of protoplasm have been advocated.

Three theories are generally recognized at the present time: the granular theory, the alveolar theory, and the fibrillar theory. Each of these theories presupposes two types of material, one liquid, the other solid or semisolid. The theories differ chiefly in the form assigned to the solid or semisolid material. According to the **granular theory** the solid or semisolid material consists of minute granules suspended in the liquid material. According to the **alveolar theory**, the semisolid is spongelike and the numerous minute spaces, called alveoli, which correspond to the pores of the sponge, are filled with the liquid material. According to the **fibrillar theory** the solid or semisolid material takes the form of fine threads, called fibrillae, which form a network extending throughout the liquid portion. It is possible that all three types of structure exist in protoplasm, depending on the conditions under which the protoplasm happens to be and the function or functions which it is performing. It may also be that all of these theories are too schematic, that the actual structure of protoplasm is more complicated, and that a third substance determines the type of structure assumed at a particular time or under a particular set of conditions.

Protoplasm possesses some of the properties of colloidal systems. However, colloidal systems as they occur outside of organisms lack many of the properties of living protoplasm. Under certain conditions protoplasm behaves as an **elastic gel**, i.e., a gel which, within limits, returns to its original shape when deformed. The investigation of nonliving elastic gels has shown that the structural units of elastic gels are fibers, possibly elongated and interlocking molecules. Observations on the structure of the cell wall and other nonliving products of protoplasm indicate a fibrous structure. These facts favor the fibrillar hypothesis. However, the fibrillae may be of many different types and those seen in fixed preparations may represent the result of the coagulation and aggregation of numerous submicroscopic fibrils, possibly each consisting of a large linear organic molecule.

The other approach is to attempt to build up from known or determinable facts and principles of organic chemistry a **theoretical structure** which could carry on the activities of protoplasm, and then to test for the existence of this structure by experiment and observation. In this discussion we are chiefly concerned with proteins since it would seem that they play the most important part in determining the structure of protoplasm. Recent work seems to show that **protein molecules** occur in two forms: a **fibrous form** present in the fibers of wool and silk, the fibers of connective tissue, and perhaps the fibrils of muscle; and a **globular form** exemplified by egg albumin. In either case there is a "backbone" of carbon, nitrogen, hydrogen, and oxygen atoms to which the amino acids are united by peptide linkages to form side chains. The properties of the different proteins are dependent on their side chains. In the case of a fibrous molecule the "backbone" is extended and forms the axis of the molecule. Connectives between their side chains cause the individual molecules to become united into fibers. In the case of globular proteins the "backbone" is folded upon itself repeatedly to form a compact mass in which some of the side chains are in the interior and some on the outside. Under certain conditions it appears that a protein with globular molecules may be changed into one of the fibrous type.

Although we are far from a complete theory of how proteins bring about the vital activities of protoplasm it appears evident that their structure offers almost infinite possibilities for complexity and variety and that they could therefore form the basis of a very complex chemical mechanism.

3. ENZYMES

In living cells chemical changes occur with very little change in temperature and with the reacting substances in moderate concentrations in water. In most cases to bring about the same changes in the laboratory with the same substances isolated from cells high temperatures and powerful agents are required. We now know that the chemical changes in living cells are made possible by the presence of substances called **enzymes**. The word "enzyme" comes from a Greek root referring to fermentation and its use as a general term is due to the fact that one of the first of these agents to be discovered and investigated was the one which occurs in yeast and brings about the fermentation of sugar to alcohol. This was at first thought to be a single enzyme and called **zymase.** It is now known that at least six or seven and perhaps more separate enzymes are concerned in the fermentation.

Enzymes have been called organic catalysts. Their action in promoting reactions between organic substances is very similar to the action of inorganic catalysts referred to in the previous chapter. Enzymes act only in water on substances dissolved or suspended in water and, in general, only under conditions similar to those which exist in organisms (see below). Some enzymes have been isolated in crystalline form. The main features of enzymes may be summarized as follows:

1. Enzymes increase the velocity of chemical reactions without them-

selves being used up in the process and without providing the energy for the reaction.

2. So far as is known, enzymes are produced only by living cells. They are probably cell proteins and as such behave as colloids.

3. Some enzymes, such as zymase referred to above, are active in living cells, while others, including those of the digestive juices, are normally passed out of the cells in which they are formed and produce their effects outside. Even when an enzyme acts only within a cell and associated with living protoplasm, the evidence shows that it should be regarded as a separate substance and not as a part of the living material.

4. Enzymes are sensitive to temperature, being destroyed by temperatures over 100°, and they are active usually only within a comparatively small temperature range. They are also sensitive to the hydronium or hydroxyl ion concentration, which must be within certain values which are different for different enzymes.

5. The action of enzymes is specific, i.e., any one enzyme furthers only one or at most a few similar reactions. The action of the enzyme is also reversible, i.e., may take place in either direction, and the direction depends on the concentrations of the reacting substances.

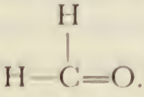
4. CELL METABOLISM

Metabolism has already been defined as the chemical changes which occur in an organism. Although not all of the chemical changes which occur in organisms occur within their cells, the cell is undoubtedly the most important seat of chemical activity in the organism. This chemical activity is not to be thought of as consisting of random reactions but rather as conforming to a system or **chemical mechanism** largely activated by enzymes and determined by the already existing structure of the protoplasm and the arrangement and quantities of raw materials which it contains. There are the building-up processes which are grouped under anabolism and the breaking-down processes grouped under katabolism, the latter in many cases associated with or involving respiration.

A. ANABOLISM

Anabolism in green plants differs from that in animals and nongreen plants, since green plants use inorganic raw materials for the synthesis of their food substances while animals and most nongreen plants are dependent on green plants for their food materials. It will be most convenient to begin with the anabolism of the green plant.

(1) ANABOLISM OF THE GREEN PLANT

The first steps in this process have already been referred to in discussing **photosynthesis** in *Spirogyra.* We are now prepared to discuss photosynthesis in more detail from the chemical point of view. The beginning and end of the photosynthetic process may be represented by the formula (Fig. 7:2). This formula records the following facts regarding photosynthesis: (*a*) Equal numbers of carbon dioxide and water molecules are used up in the process. (*b*) The process occurs only in the presence of light. (*c*) The number of oxygen molecules given off is equal to the number of carbon dioxide molecules used up. When, in the above formula, *n* is made equal to unity the product on the right is formaldehyde, H_2CO or  $H-\overset{\displaystyle H \atop |}{C}=O$. It is thought that the formation of formaldehyde may be the first step in photosynthesis. However, satisfactory proof of this is lacking. Objections to the formaldehyde theory are: (*a*) Formaldehyde is known to be poisonous to plant cells even in very great dilutions. (*b*) Formaldehyde has not been found in recognizable quantities in plants. These two objections may be met by assuming that the formaldehyde as formed is immediately changed to sugar. The change from formaldehyde to sugar may be represented as in Fig. 7:3.

$$nCO_2 + nH_2O + \text{Light energy} \longrightarrow C_nH_{2n}O_n + nO_2$$

Fig. 7:2 Formula illustrating photosynthesis. Light energy is absorbed in the process.

$$\underset{\text{Formaldehyde}}{6\,HCHO} \longrightarrow \underset{\text{Glucose}}{C_6H_{12}O_6}$$

Fig. 7:3 Polymerization. In the formation of glucose by this method six molecules of formaldehyde combine.

This process is one which can be carried out in the laboratory outside of the cell and is an example of **polymerization,** a general term applied to a reaction in which molecules of a single substance are combined or condensed into a single molecule.

No theory of photosynthesis can be regarded as satisfactory until it can be put to the test of experiment and carried through under controlled conditions in the laboratory. That this has not yet been done is probably due to a feature which is common to most chemical processes carried on in cells, viz., that they do not consist of a single reaction but of a series of reactions which follow closely upon each other, the various steps occurring on a molecular scale. So far it has not been found possible to imitate such conditions in glass vessels in the laboratory.

Photosynthesis is the most fundamental of all anabolic processes. It is practically the only method by which energy from the external environment can be converted into potential chemical energy in the cell.[1] The energy for all other vital processes is obtained, in practically every case, by the oxidation of the glucose or some other monosaccharide formed in photosynthesis, or the oxidation of materials built up by means of energy obtained from the oxidation of such monosaccharides. Thus when two molecules of glucose are synthesized to form a molecule of maltose with the liberation of a molecule of water (Chap. 6, Art. 1) the small amount of energy required must come from the oxidation of glucose. Also when starch is formed by the synthesis of disaccharides the energy comes from a similar source. All of the various steps indicated in the synthesis of carbohydrates including photosynthesis in plants require enzymes. They require a particular combination of specific enzymes. Photosynthesis may also be regarded as the method by which carbon is made available for use in organisms.

Fats and fatty acids are formed from glucose. The process is somewhat complicated. A large number of steps and corresponding enzymes are involved. The chemical reactions which apparently occur include polymerization and dehydration (loss of water molecules with or without further synthesis).

For the synthesis of proteins nitrogen is necessary. Plants are the only organisms which can utilize inorganic nitrogen. Certain bacteria are able to utilize the nitrogen of the atmosphere and transform it into nitrates or nitrites. These bacteria will be discussed later in the chapter on bacteriology. All other plants must obtain their nitrogen either from these bacteria or from the soil in the form of nitrates or ammonia. The nitrates and ammonia reach the soil largely as the result of the decay or breakdown of protein material from plants and animals. There is thus a nitrogen cycle (see Chap. 9). The raw materials for the synthesis of proteins in green plants are glucose, which provides the carbon, hydrogen, and oxygen, and inorganic ions, including ammonium, nitrate, phosphate, and sulphate ions (see Chap. 5).

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[1] There are certain bacteria which obtain energy for the synthesis of food materials from the oxidation of inorganic materials, a process which has been called chemosynthesis; but they do not appear to occupy a significant place in the food cycle being described.

(2) ANABOLISM IN ANIMALS AND NONGREEN PLANTS

All of the raw materials used by the cell must pass into it through the plasma membrane. Hence to be used by animals and nongreen plants the carbohydrates, fats, and proteins manufactured by green plants must be reduced to soluble substances. This means that the starches must be reduced to simple sugars, usually monosaccharides, the fats to fatty acids and glycerine, and the proteins to amino acids. After passing through the plasma membrane these materials are then **resynthesized** in the cell by the protoplasm and the enzymes contained in it into the specific carbohydrates, fats, and proteins peculiar to the particular cell.

B. *KATABOLISM*

So far as is known katabolism is similar in plants and animals excepting that in general it is more prominent in animals because of their greater activity. Katabolic processes, like anabolic processes, are usually activated by enzymes. Katabolism is usually closely linked to **respiration.** But this is not always so, as for example in the contraction of a muscle, where the first burst of energy which causes the contraction is due to an organic decomposition which does not require oxygen. The katabolism of **carbohydrates** usually involves hydrolyses and oxidations. The end products of the series of reactions are carbon dioxide and water. **Fats** also are broken down to yield energy. Here also hydrolysis plays an important role and the end products are carbon dioxide and water. Oxygen is required for these reactions and they occur only in conjunction with respiration.

The actual breaking down of **proteins** probably occurs only as the result of wear and tear of protoplasm or when a part of a cell or an entire cell is replaced in the development of an organism. Proteins break down into amino acids. However, not much energy is yielded by the reactions which are mainly hydrolyses. On the other hand, the katabolism of amino acids yields energy, which is almost equal in amount per gram weight of amino acid to the energy yielded by the same weight of carbohydrates. The deaminization of amino acids by which they are decomposed into ammonia, NH_4, and a simpler organic acid is illustrated in Chap. 6. This is also an oxidation and is dependent on respiration. The ammonia is excreted as urea, $CO(NH_2)_2$.

5. FUNCTIONS OF THE NUCLEUS

The problem of the function or functions of the nucleus has been attacked by two methods, one observational, the other experimental. The description of mitotic division must have made it clear that the nucleus plays an important role in cell division. The study of heredity and the behavior of the chromosomes in the germ cells makes it clear the nucleus is the main, if not the only, part of the cell concerned with the transmission of hereditary characters. For information regarding the relation of the nucleus to the general activity and metabolism of the cell, resource is had to experiments in which the cell is divided into two portions, one of which is without a nucleus, while the other contains the nucleus of the cell. The experiment can be performed without great difficulty on an amoeba using a fine glass needle and a micromanipulator. A plasma membrane forms over the cut surface of each portion and each part will continue to show amoeboid movement. Indeed the enucleate part may not only move but also respire and respond to stimuli — all of which may be regarded as katabolic activities. The enucleate part is, however, incapable of growth or the regeneration of a new nucleus. There is much to support the thesis that the nucleus is the seat of the formation of many enzymes which pass through the nuclear membrane and activate reactions in the cytoplasm. In this way it may be said to control the activities of the cell.

6. CHEMICAL CYCLES

The chemical elements which enter into the composition of organisms may be regarded as passing through cycles in one phase of which they are incorporated in the bodies of various organisms and in another phase of which they form a part of the lifeless matter of the earth. A good example is provided by carbon.

The wanderings, unions, and separations of a carbon atom would make a fascinating story. In the diagram (Fig. 7:4) these wanderings are represented as occurring in a cycle although in most cases the path of an individual carbon atom is long and devious. Let us for the moment disregard time and space and follow an atom of carbon round the cycle. Starting in the atmosphere as part of a molecule of CO_2, it some time or other will encounter a green plant and enter one of its green cells, where it will be swept up by a chloroplast and put through the process of photosynthesis, emerging as one of the atoms of a sugar molecule. The carbon atom of the sugar molecule may be stored away in a starch granule, to be later converted back into sugar, or participate in the formation of new protoplasm, or enter into the composition of a molecule of cellulose to be built into a cell wall. In the protoplasm it may take part in respiration and be returned to the atmosphere again as CO_2.

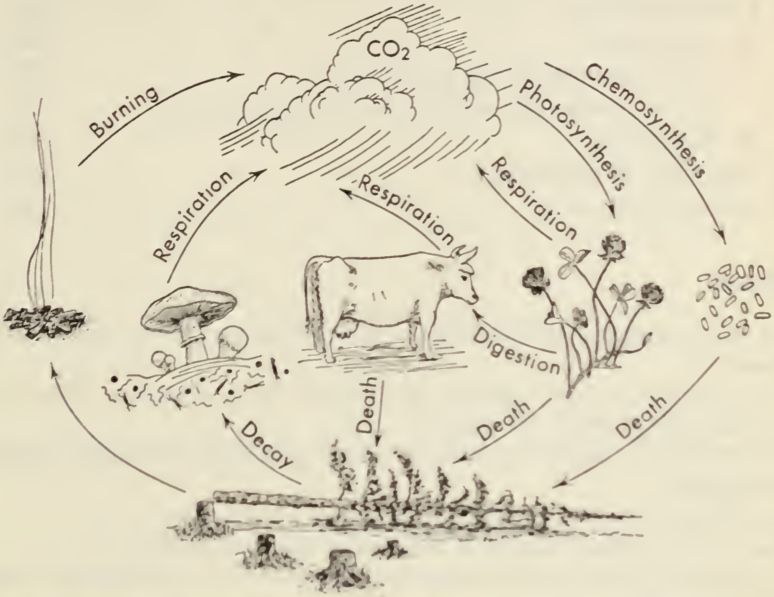

Fig. 7:4 Diagram of the carbon cycle.

If the plant is eaten by an animal, the plant tissues will be digested and the carbon atom absorbed and assimilated into the body of the animal. From here the persistent little carbon atom may go on many and exciting journeys which end either in the atmosphere through respiration or in the dead body of some animal or plant. If the dead body of the plant or animal decays, the carbon atom may become involved in the process and return to the atmosphere in a molecule of carbon dioxide. If the plant or animal becomes buried in a peat bog, the carbon atom may become an atom of coal. When the coal is burned, the carbon atom is again returned to the atmosphere.

Most of the carbon which occurs on the earth's surface or in the rocks of its crust has been at one time or another a part of some organism and some of it has passed in succession through many organisms. Coal and graphite, which are nearly pure carbon, are the remains of ancient forests. The calcium carbonate of limestones and marble once formed shells and bones. Other elements, such as nitrogen and oxygen, which are contained in protoplasm may also be said to have cycles, some of which will be considered in later sections.

Topical Outline of Chapter 7

1. The plasma membrane 180
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3. Enzymes 185
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    A. Anabolism 186
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        (2) Anabolism in animals and nongreen plants 189
    B. Katabolism 189
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6. Chemical cycles 190

Questions

1. Can you imagine a cell without a cell membrane? Give reasons for your answer.
2. Try to picture in your mind the structure of protoplasm. Why is living material not (*a*) solid, (*b*) gaseous?
3. Why would you expect to find the most complicated chemical elements in protoplasm?
4. How does an enzyme differ from an inorganic catalyst?
5. What is the original source of the energy for vital processes?
6. To what extent can photosynthesis be carried out in the laboratory outside of the living cell?
7. Can a fat or a protein be utilized directly as such by a cell? Explain your answer.
8. State the functions of the nucleus, giving the experimental evidence for each function.

Suggestions for Further Reading

Amberron, William R., and Dietrich C. Smith, *Outline of Physiology*, F. S. Crofts & Co., New York, 1939. Chaps. 2–5. An interesting elementary discussion of the living cell.

Heilbrunn, L. V., *An Outline of General Physiology*, W. B. Saunders Company, Philadelphia, 1945. Chaps. 10–22.

PART II. Plant Life

"The green plant is the laboratory in which is manufactured food that supports practically all the higher terrestrial forms of animal life."

S. J. Holmes

CHAPTER 8

The Thallus Plants (Phylum Thallophyta, Exclusive of the Bacteria)

This chapter will be devoted to a consideration of the Thallophyta, the first of the four phyla of the plant kingdom. As outlined in the chapter on the classification of plants the phylum Thallophyta is divided into the two subphyla, Algae and Fungi. The bacteria which constitute one of the classes of the Fungi (class Schizomycetes) are reserved for a special chapter (Chap. 9).

1. THE ALGAE

The majority of the Algae are adapted to living either in the sea, where the greatest number and variety of species occur, or in fresh water. The plant body consists of a single cell or aggregate of cells showing little if any differentiation into tissues and without true roots, stem, or leaves. The subphylum is divided into four classes: Cyanophyceae or blue-green algae, Chlorophyceae or green algae, Phaeophyceae or brown algae, and Rhodophyceae or red algae.

A. THE BLUE-GREEN ALGAE (CLASS CYANOPHYCEAE)

The algae of this class are widely distributed in both fresh and salt water. At times they occur abundantly in lakes and reservoirs and their decay is one of the common causes of disagreeable odors and tastes in water supplies. A salt-water species is partly responsible for the color of the Red Sea. But the layman is more likely to have seen them on damp soil where they often form a thin dark layer on the surface or on the rocks or stones bordering a stream. Some species live at remarkably high temperatures, occurring in hot springs such as those of Yellowstone Park. Although referred to as blue-green, their color may be yellow, orange, pink, red, violet, purple, brown, or black (Fig. 8:1).

(1) OSCILLATORIA

One of the commonest filamentous blue-green algae is *Oscillatoria* (Fig. 8:1) which occurs on damp soil and in temporary pools. At each end of the filament is a hemispherical cell which forms a buttonlike cup. The other cells have the shape of short cylinders or discs. The outer cell walls are covered with a thin gelatinous coat. The protoplasm of each cell is differentiated into a clear inner portion, the **central body,** and an outer portion which contains the characteristic pigment. The central body stains with the dyes which stain chromatin but is not surrounded by a nuclear membrane and is therefore not regarded as a nucleus.

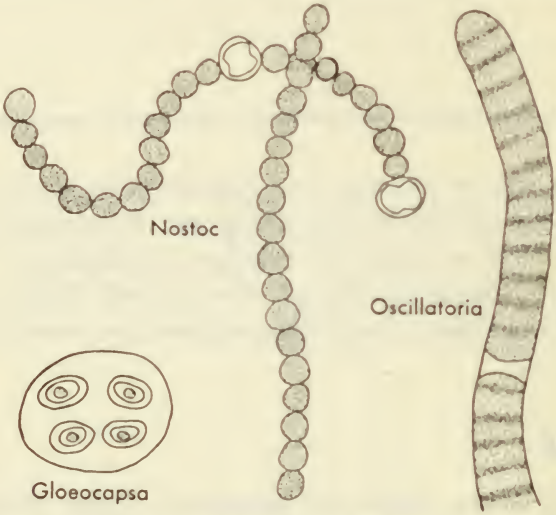

Fig. 8:1 Three species of blue-green algae (class Cyanophyceae). Redrawn after Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

The name of the genus is due to the waving or oscillatory movements which the filaments frequently show — a movement the mechanism of which is unknown and which is not characteristic of the Cyanophyceae as a whole.

The filaments grow in length by transverse divisions of the cells. From time to time gelatinous discs are formed between some of the cells and the filament breaks into sections, each of which is capable of continuing its growth. Sexual reproduction is unknown in the group.

(2) THE BLUE-GREEN ALGAE AS A GROUP

The Cyanophyceae are regarded by many botanists as a very simple group of plants related to the bacteria with which they have some characteristics in common, viz., lack of a definite nucleus, capacity of some species to "fix" the nitrogen of the air (see later under Bacteria).

B. THE GREEN ALGAE (CLASS CHLOROPHYCEAE)

The green color of these algae is due to chlorophyll and another green pigment, both of which are contained in special bodies called **chloroplasts.** The class is a large one and well illustrates certain biological principles. Several examples will be described.[1]

(1) ULOTHRIX

Ulothrix is commonly found attached to rocks or stones in cool streams or ponds where the water does not become stagnant. The plant body of *Ulothrix* consists of an unbranched filament resembling that of *Spirogyra* (Fig. 8:2). The cells of the filament are, however, shorter and the chloroplast is in the form of a plate or band. At one end is an elongated cell without chlorophyll which forms a **holdfast** by which the plant is attached.

Ulothrix reproduces asexually by means of **zoospores** (Fig. 8:2). Any cell of the plant with the exception of the holdfast cell may form zoospores. Preliminary to the formation of zoospores the entire protoplast of a cell shrinks within its cell wall and becomes rounded. The protoplast may, then, either develop directly into a zoospore by forming four flagella at one end and near them a red eyespot, or it may first divide while still within its cell wall into two, four, or as many as eight smaller protoplasts which then develop into zoospores, each with four flagella and an eyespot. The zoospores are without cell walls. They swim out of the old cell through an opening in the wall. After swimming about for a time they attach themselves to some object by their flagellated ends and develop into filaments.

In sexual reproduction the formation of **gametes** is similar to the formation of zoospores. The gametes are, however, smaller and there are more of them, sixteen to sixty-four being formed from a single protoplast (Fig. 8:2). Each has an eyespot like a zoospore, but only two flagella instead of four. The gametes leave the old filament cell by an opening and swim about. They are all alike, there being no differentiation into male and female. Such gametes are called **isogametes.** They fuse together in pairs forming **zygotes** (Fig. 8:2). Each zygote then becomes surrounded by a resistant cell wall. It is in this condition that the plant passes through the winter or other unfavorable season. When a zygote germinates it produces a number of zoospores, each of which develops into a new filament similar to the filaments in which zoospores and the gametes were formed.

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[1] *Spirogyra*, which belongs to this group, is described in Chap. 4.

(2) OEDOGONIUM

Oedogonium is another unbranched green alga which occurs in fresh-water ponds, sometimes attached and sometimes floating at the surface. The filament, like that of *Ulothrix* and *Spirogyra*, consists of cylindrical cells arranged end to end. Each cell when mature contains a large central vacuole which is surrounded by cytoplasm containing a single nucleus and an irregularly shaped chloroplast. The filament grows in

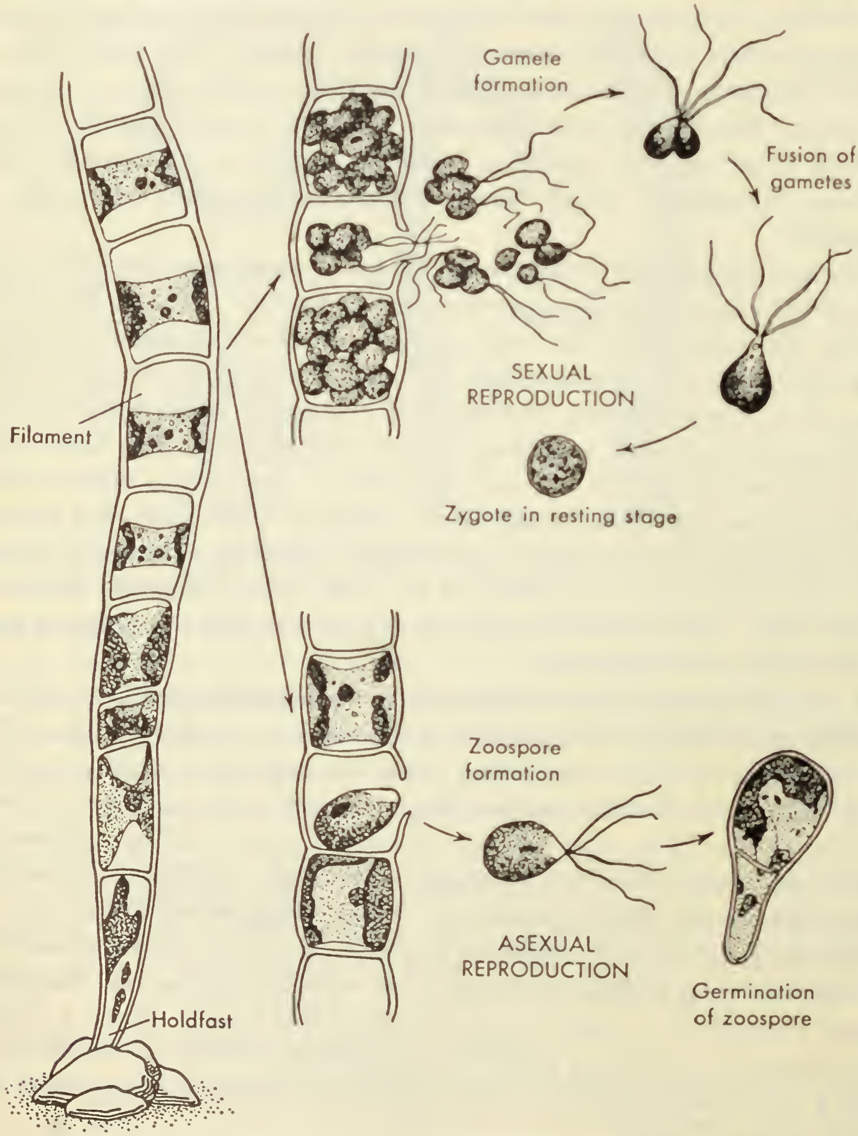


Fig. 8:2 Life cycle of *Ulothrix*. On the left a filament attached to some stones. To the right above, sexual reproduction; below, asexual reproduction. Redrawn after Altmans.

length by transverse division of certain of its cells, not every cell being able to take part in the growth.

Asexual reproduction occurs by means of **zoospores.** When a zoospore is to be produced the entire protoplast increases in size, and causes the side walls of the cell to bulge. The chloroplast then recedes from one end of the cytoplasm, making this end colorless. In a circle, around the colorless end, a ring of cilia is developed. The cell wall of the old filament cell breaks open and the zoospore, which is without a cell wall, emerges. After swimming for a time the zoospore comes to rest. Its clear ciliated end develops into a holdfast and becomes divided off as a separate cell. The rest of the zoospore forms a new *Oedogonium* filament. Thus the asexual reproduction of *Oedogonium* is not unlike that of *Ulothrix*.

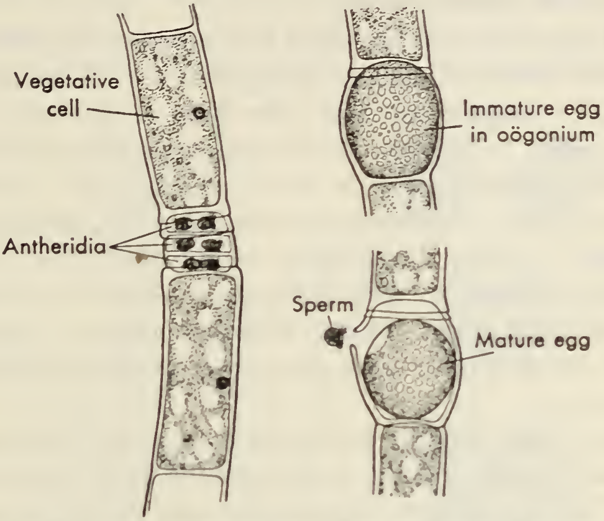


Fig. 8:3 *Oedogonium.* Sexual reproduction. Redrawn after Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

In sexual reproduction of *Oedogonium* the gametes are formed by special modified filament cells (Fig. 8:3). The cells in which the male gametes are formed, called **antheridia,** arise by rapid cell division and are much shorter than the ordinary filament cells. The protoplast within each of these cells either becomes transformed directly into a male gamete or **sperm,** or divides giving rise to two sperms. The male gametes are similar to the zoospores, but smaller in size. Each female gamete or egg is formed by the enlargement of a special filament cell, called an **oögonium,** the protoplast of which after being filled with food materials becomes spherical. **Fertilization,** the union of the sperm and egg, is made possible by a pore in the side of the cell wall of the oögonium through which the sperm enters (Fig. 8:3). Gametes which differ as do the egg and sperm of *Oedogonium* are said to be **heterogametes.** As in *Ulothrix* the zygote of *Oedogonium* develops a resistant cell wall in which it tides over unfavorable conditions. When it germinates it forms by division four zoospores.

(3) THE DIFFERENTIATION OF THE GAMETES AND THE BEGINNING OF SEX IN THE GREEN ALGAE

A series of stages may be obtained by arranging the plants studied in the order of the differentiation of their gametes. In *Ulothrix* the gametes are exactly alike (**isogametes**) and differ from zoospores only in size and number of flagella. In *Spirogyra*, while any cell of a filament may become a gamete, the gametes differ in their behavior, one, which may be designated as female, remaining in its own filament, the other which we may call male, moving through the conjugation tube to the female gamete. A high degree of differentiation is shown in the gametes of *Oedogonium*. In these plants the egg, or female gamete, is large and nonmotile while the sperm, or male gamete, is small and motile (**heterogametes**).

We will see later that the important feature of sexual reproduction is the union of two nuclei. Hence, provided the sperm contains a nucleus, it may have little cytoplasm. When this occurs the egg is usually large, containing the cytoplasm and food materials necessary for the development of the young plant. The advantage of this differentiation, leading to the formation of heterogametes, lies in the fact that in one gamete, the egg, the cytoplasm may be organized for the storage of food materials, while in the other gamete, the sperm, it may be specialized for locomotion.

(4) *PROTOCOCCUS*

Everyone has seen green areas, due to this organism, on the bark of trees, fences, and even pieces of stone, but not everyone realizes that the green color is due to a small green plant, the scientific name of which is *Protococcus* (Fig. 8:4). Not until a speck of this thin layer is scraped off, placed under the microscope, and examined carefully does this become apparent. The green speck is then found to be composed of hundreds of minute spherical cells all very much alike, adhering to form small, irregular groups. Each cell of *Protococcus* leads its own independent life and is in fact an individual plant. *Protococcus* is chosen for study because it is easily obtainable and because, as the green coloring on the trunks of trees, it is a familiar object. However, its habitat, i.e., the place and conditions of its occurrence, is somewhat exceptional since most of the simple green plants live in water.

Each cell of *Protococcus* is surrounded by a more or less rigid cellulose **cell wall** which gives the cell a fixed shape. The protoplasm fills the interior of the cell. One or occasionally two large **chloroplasts** almost fill the **cytoplasm,** leaving a clear region in the center in which the relatively small **nucleus** is located.

If the cells from a group of *Protococcus* are examined, it will be found that some of them show evidence of dividing into two equal portions. First the nucleus divides into two nuclei which move apart from each other, then a new cell wall is formed between the nuclei separating the cytoplasm into two parts, each containing a single nucleus. The two daughter cells may adhere together and each may itself divide, so that groups of four or even eight or more cells may be found. This process which is a form of asexual reproduction is called **simple fission.** In this case the parent cell which divides does not die, although it loses its individuality by becoming two individuals. Death occurs in *Protococcus* only as the result of adverse external conditions.

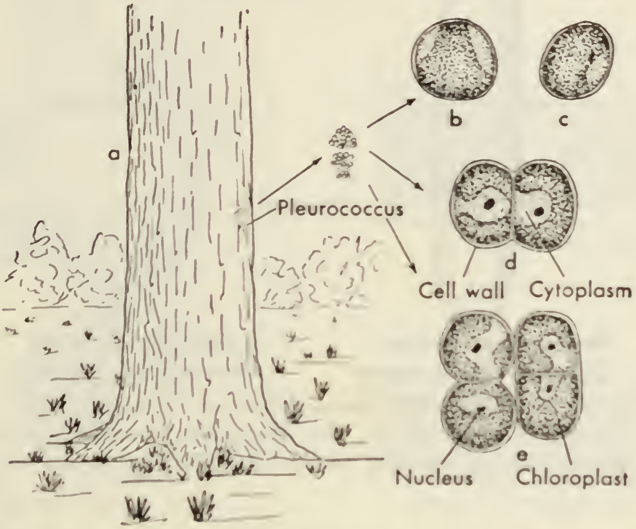


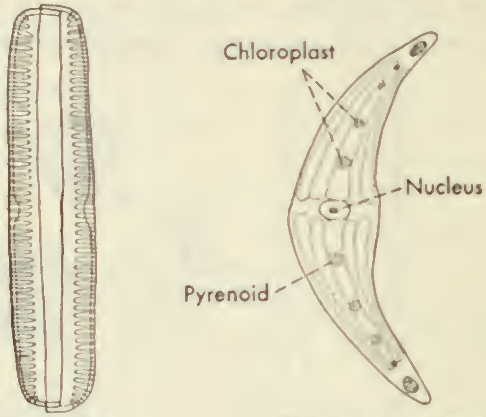
Fig. 8:4 *Protococcus. a,* plant growing on the bark of a tree; *b* and *c,* single-celled stages; *d,* two cells which have resulted from the division of a single cell; *e,* group of four cells. *b–e,* highly magnified.

(5) THE DESMIDS

Desmids are interesting because of their frequent occurrence in fresh water and the fanciful shapes which the cells assume. Each consists of a single bright green cell often constricted in the center (Fig. 8:5).

(6) THE DIATOMS

The diatoms (Fig. 8:5) are unicellular algae of uncertain systematic position, being classified by some as brown algae, while others regard them as closely related to the green algae. The cell wall consists of two halves or **valves** impregnated with silica. They are frequently a very important component of the plankton of the sea and of lakes and ponds. In the sea they are one of the main sources of food for marine animals.



Pinnularia, a diatom
The case only is shown

Closterium, a desmid
showing cell contents

Fig. 8:5 A diatom, *Pinnularia*, and a desmid, *Closterium*. *Pinnularia* redrawn after Smith, Overton *et al.*, *Textbook of General Botany*, The Macmillan Company; *Closterium* redrawn after Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

(7) ULVA

The sea lettuce, *Ulva*, which is particularly abundant on the seashore near where fresh water enters the sea and is often conspicuous by its bright green color, is an example of an alga which forms a typical thallus (Fig. 8:6). The thin filmy-frilled thallus of this plant is soft and flexible so that when left by the receding tide it adheres closely to the rocks or pebbles to which it is attached. The attachment to the rocks or pebbles is made by means of a slender stalk which is expanded into a small attachment disc. A thin section cut across the thallus (Fig. 8:6) shows it to be composed of two layers of exactly similar cells, each having a protoplast containing a nucleus and a chloroplast. Near the stalk and in the stalk itself certain cells are elongated into tubes which grow down between the two layers in the stalk and into the attachment disc.

(8) THE EVOLUTION OF THE MULTICELLULAR BODY

The simplest green algae, of which *Protococcus* is an example, consist of a single cell. Next in order are the filamentous forms, like *Spirogyra*, in which the cells of the filament are all alike and carry on their vital processes independently. Closely following these are plants like *Ulothrix* in which one of the cells of the filament is without chlorophyll and is differentiated to act as a holdfast. In each of these two types any cell of the filament is capable of dividing and forming other filament cells. A further step in cell differentiation is seen in *Oedogonium* where not all the cells can carry on this function. In the sea lettuce, *Ulva*, there is a well-developed thallus of considerable size, which, however, is relatively simple in its cellular structure. The above are all green algae and may be considered to be related forms although it is unlikely that we have here any actual line of descent.

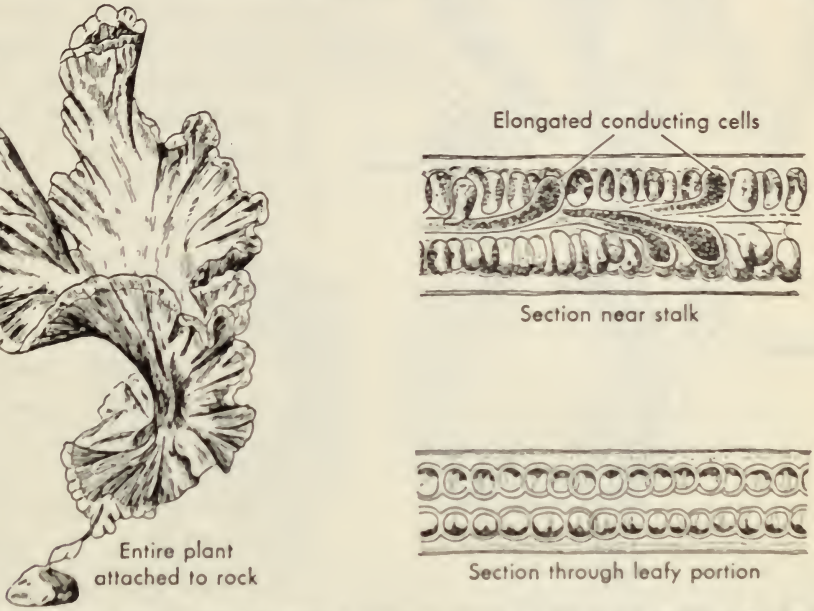

Elongated conducting cells
Section near stalk
Entire plant attached to rock
Section through leafy portion

Fig. 8:6 *Ulva*, sea lettuce. On the left, an entire plant; on the right, sections across the thallus. Redrawn after Bower, *Plant Life on Land*.

(9) THE GREEN ALGAE AS A GROUP

The preceding discussion has shown that the green algae (Fig. 8:6) are a large and varied group of great importance in the evolution of the higher plants and in the life of fresh water and the sea.

C. *THE BROWN ALGAE (CLASS PHAEOPHYCEAE)*

A common brown alga of our seaboard is the rockweed, *Fucus*. It is found between the levels of low and high tide. One end is attached to a rock or pebble by a holdfast while the rest of the thallus floats in the water, buoyed up by small air sacs or bladders in its branches. At low tide it is left high and dry except for the water which it retains within the folds of its flat, narrow branches. All who have walked along the shore at low tide are familiar with the brown leathery carpet which *Fucus* makes over rocks and stones. Its surface, like that of many seaweeds, is slippery. The greater portion of the thallus, however, consists of broad flat leaflike branches (Fig. 8:7). At the tip of each branch is an oval depression at the bottom of which is an **apical cell.** The branch is added to by the growth and differentiation of cells arising from the division of the apical cell. After a branch has reached a certain length, the apical cell divides equally into two cells each of which becomes a separate apical cell. As growth continues the branch becomes forked. Each of the branches of the fork grows to the usual length and then in turn becomes forked. This method of branching is called **dichotomy.** On the branches are the **air bladders.**

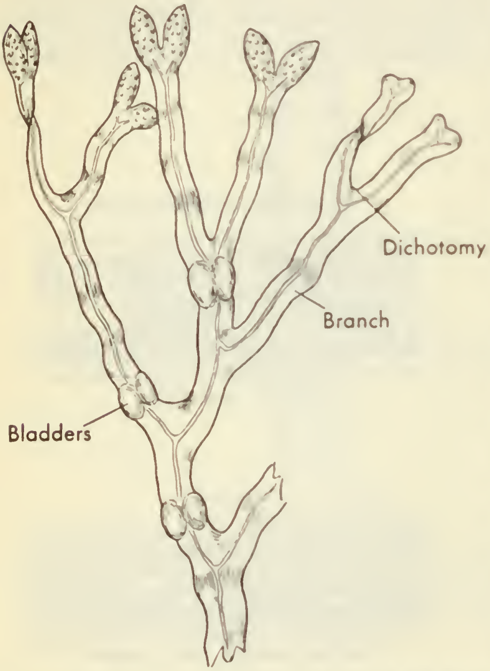


Fig. 8:7 *Fucus*, a rockweed. Part of the thallus. Redrawn after Smith, Overton *et al.*, *Textbook of General Botany*, The Macmillan Company.

A cross section of the thallus shows it to be composed of an external portion or **cortex** and an internal, central portion, the **medulla.** The cells of the cortex are arranged with their long axes at right angles to the surface and the outer walls of the cortex cells form a thick protective covering for the thallus. The cells of the medulla are filamentous and form a tangled mass through which food materials are conducted. The chlorophyll is in chloroplasts in the cells of the cortex. Its green color is somewhat masked by the presence of a brown pigment. The "air bladders" are enlarged intercellular spaces containing, chiefly, carbon dioxide gas.

Asexual reproduction by means of spores or other reproductive bodies is unknown in *Fucus* and its near allies. Occasionally plants may be torn apart and the pieces regenerate new individuals. However, sexual reproduction is the usual method. Sex organs occur on the ends of free branches. The actual organs develop in cavities called **conceptacles** (Fig. 8:8) which open to the exterior by means of pores called **ostioles.** The formation of conceptacles causes the tip of the branch to swell. In some species of *Fucus*, including the common Eastern species, *Fucus vesiculosis*, the male and female sex organs are produced in different conceptacles. In other species both sex organs occur in the same conceptacle. A male sex organ or **antheridium** (Fig. 8:8) consists of a large ovoid cell born on a filament which grows out from the wall of the conceptacle. The nucleus of the antheridial cell divides into two, four, and so on, until a total of sixty-four nuclei are formed. After this has been accomplished the cytoplasm divides and the sixty-four resulting cells become **sperms.** A female sex organ or **oögonium** (Fig. 8:8) consists of an enlarged spherical cell on the end of a short stalk cell. The cytoplasm of the oögonial cell becomes filled with reserve materials after which its single nucleus divides into two, four, and finally eight nuclei. The cell then divides forming eight spherical **eggs.** Both eggs and sperms pass out through the ostioles into the sea where fertilization (Fig. 8:8) occurs.

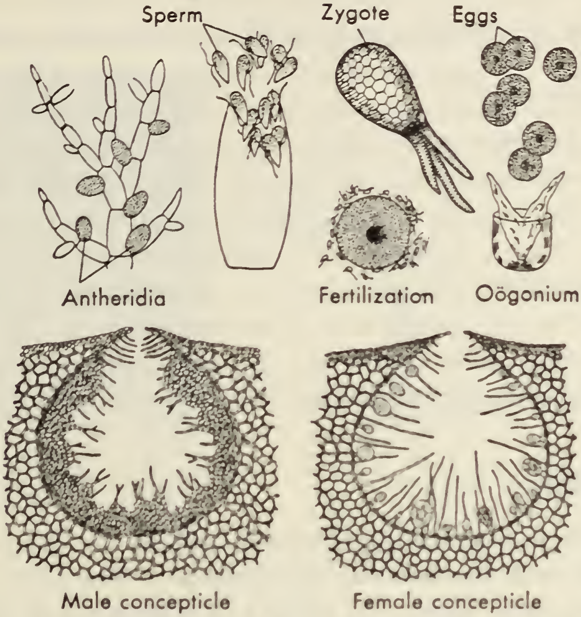


Fig. 8:8 *Fucus.* Sexual reproduction. Lower left, section of a male conceptacle containing antheridia. Upper left, several antheridia on a branched filament, one of which is enlarged to show sperm escaping. Lower right, section of a female conceptacle containing oögonia. Upper right, eggs escaping from an oögonium, fertilization, and a young zygote. Redrawn after Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The zygote develops (Fig. 8:8) immediately into a new *Fucus* plant. It will have been noticed that the sex organs, antheridia and oögonia, each consist of a single cell. This is typical of the Division Thallophyta.

D. THE RED ALGAE (CLASS RHODOPHYCEAE)

Since nearly all red algae occur in the sea below low-water mark they are not familiar to many laymen. Certain members of the class, notably *Polysiphonia*, a plant with numerous slender branches, are of considerable scientific interest since their life cycles show the alternation of two generations, one of which reproduces sexually and the other only asexually. This is a condition which we shall find occurs in mosses and ferns and all of the higher plants. However, it is doubtful whether the red algae are to be regarded as the ancestral forms of these plants. An adequate discussion of the matter would take us beyond the scope of this text. One group commonly called **corallines** deposit calcareous material in their cell walls and are in part responsible for many "coral" reefs.

2. THE FUNGI

The student is referred to Chap. 3 and to the Appendix for the characteristics and classification of the group. The first class, Schizomycetes or bacteria, forms the subject of a separate chapter (9). The second class, Myxomycetes, will not be considered further in this text. Examples of the next three classes, the Phycomycetes or algal fungi, the Ascomycetes or sac fungi, and the Basidiomycetes or basidia fungi will be described.

A. THE PHYCOMYCETES

(1) THE BREAD MOLD, *RHIZOPUS*

(a) THE MYCELIUM

Everyone has seen this common mold on stale bread or decaying fruit. At first the mold appears as a gray fuzz on the surface of the bread; later as the spores formed by it become darker and eventually almost black the mold takes on this color (Fig. 8:9). The gray fuzz, which appears like a layer of finely teased out absorbent cotton, consists of numerous fine filaments, which in the case of a fungus are called **hyphae.** To the mass of hyphae which make up the plant body of a fungus the term **mycelium** is applied. The mycelium of the bread mold is not divided into cells. The protoplasm takes the form of a continuous mass extending through the hyphae and contains numerous nuclei. The general term **coenocyte** is applied to such a plant body or portion of a plant body in which the protoplasm contains many nuclei and is not divided into separate cells. Some of the hyphae grow down into the starchy substance of the bread secreting as they go an enzyme which digests the starch. Thus the bread serves both as a substratum upon which the fungus grows and as the source of its food. The mold spreads over the bread by sending out slightly larger hyphae called **stolons** which grow over the surface (Fig. 8:9). Where the stolons touch the bread, they branch and give rise to hyphae, some of which dip down into the substance of the bread while others grow upward.

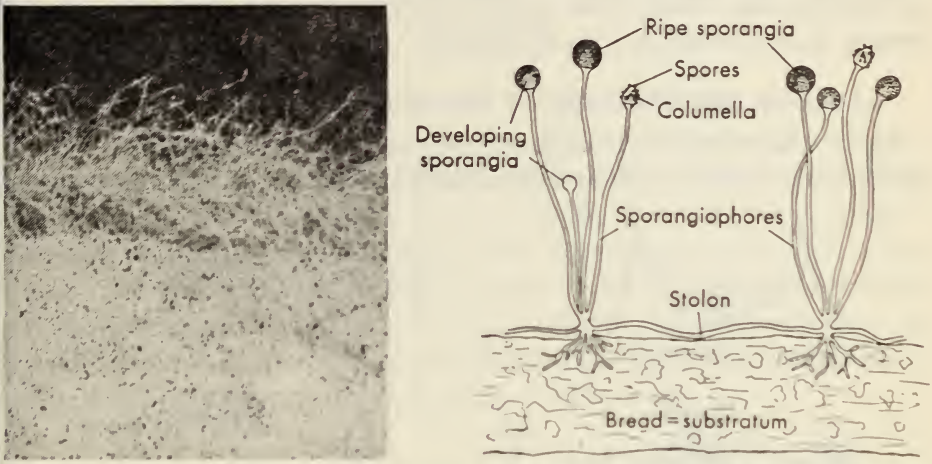


Fig. 8:9 *Rhizopus nigricans*, a bread mold. At left, a photograph of the edge of a slice of bread over which the mold has spread. The black dots are ripe sporangia. On the right, a diagram illustrating the structure of the mold.

(b) ASEXUAL REPRODUCTION IN RHIZOPUS

On the tips of the erect hyphae which grow up from the stolons of the bread mold round bodies called **sporangia** develop. For this reason these hyphae are called **sporangiophores**. A **sporangium** (Gr. *sporos*, a spore + *aggeion*, a receptacle) is a structure in which spores are formed. In a sporangium of the bread mold an outer or peripheral portion is separated from an inner portion, called the **columella**, by a partition. The protoplasm of the columella is continuous with that of the hypha. The protoplasm of the peripheral portion of the young sporangium divides and forms **spores.** The spores of the bread mold, like the hyphae from which they arise, consist of masses of protoplasm in which there are usually several nuclei, the whole being surrounded by a resistant wall. When the process of spore formation is completed, the fragile outer wall of the sporangium bursts open and the spores are liberated. When a spore arrives on a suitable substratum it germinates, sending out a hypha which develops into a mold. The very special conditions, i.e., the moist surface of bread or decaying fruit, required by the bread mold for its development necessitate the production of reproductive bodies which will become widely distributed. The minute spores remain suspended in the air for long periods of time and are easily blown from one surface to another and attain such a wide distribution that they are usually present where bread or fruit is exposed.

(c) SEXUAL REPRODUCTION IN RHIZOPUS

In the common bread mold there occurs what corresponds to a separation of the sexes. Some strains, called **plus strains,** produce gametes of one kind while other strains, called **minus strains,** produce gametes of another kind. The differences between the strains and the differences between their gametes seem not to be accompanied by any visible an-

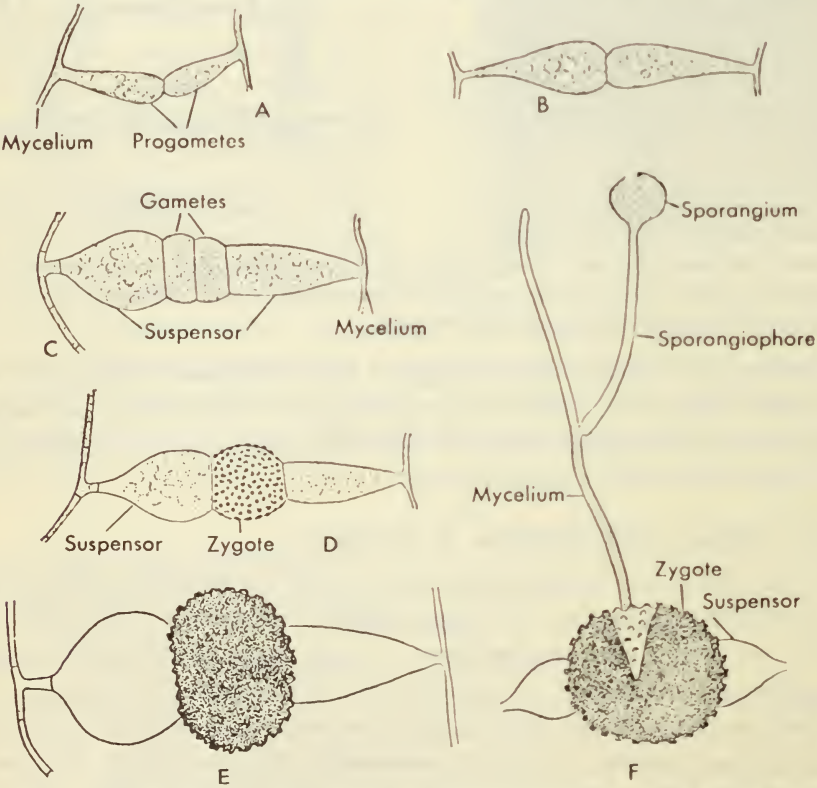


Fig. 8:10 *Rhizopus nigricans*, a bread mold. Sexual reproduction. A–C, fusion of gametes; D–E, formation of zygote; F, germination of zygote. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

atomical differences. Only gametes of different strains, i.e., plus and minus, will unite to produce a zygote. If plants of different strains grow together, so that their hyphae intermingle, gametes are formed. The gametes arise from short club-shaped lateral branches (Fig. 8:10). When the lateral branches from two hyphae of plants of opposite sign meet, a cell is separated off at the end of each. These cells then fuse to form zygotes. Each zygote then develops a thick resistant cell wall and may remain dormant for a time, after which, if conditions are favorable, it germinates and develops into a new plant.

(2) OTHER PHYCOMYCETES

One common group of Phycomycetes (order Saprolegniales) grows in ponds and streams on the dead bodies of fish and insects. Another group (order Peronosporales), which includes the "downy mildews" is parasitic on plants. A third group (order Mucorales) includes the black mold described above. A fourth group (order Entomophthorales) attacks living insects and includes the fly mold, the effects of which are sometimes seen on windowpanes when the flies, dead or in an advanced stage of the disease, are surrounded by a white halo.

B. THE ASCOMYCETES

(1) THE CUP FUNGI

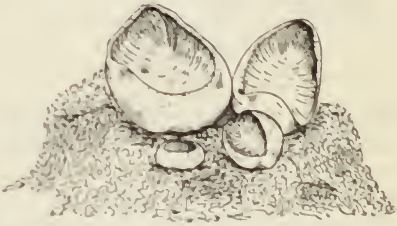


Fig. 8:11 Cup fungi (class Ascomycetes). Redrawn after Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

Probably the most familiar members of this class are the delicate little "cup fungi" often seen on decaying tree stumps. In a common species, *Peziza coccinea*, the inside of the cup is bright red, in other species it is yellow, orange, or even bluish. The tissue lining the cup is called the **hymenium** and it is here that the sacs or **asci,** each containing eight **ascospores,** are formed. The asci are known to be formed as the result of a sexual process (Fig. 8:11).

(2) THE POWDERY MILDEWS

Another important group of Ascomycetes are the powdery mildews which are all parasitic, chiefly on the leaves of higher plants. The mycelium, which consists of hyphae, forms a whitish network on the surface of the leaves and sends branches called **haustoria** into the cells of the leaf. Hyphae also grow out from the leaf at right angles to its surface. These are called **conidiophores** since they bear a special kind of spore called a **conidium.** The conidia develop at the ends of the conidiophores by transverse division and, when numerous, form a powdery patch on the leaf.

Sexual reproduction occurs late in the season and the resulting "spore fruits" enable the parasite to survive the winter. Two short hyphae grow up side by side and come into contact. A nucleus from one of the hyphae, which may be called an **antheridium,** moves into the other hyphae, the **oögonium,** and fuses with a nucleus there forming a zygote (Fig. 8:12). Cells from the stalk of the oögonium now grow up around the zygote and enclose it, forming a rounded spore fruit. The enclosed zygote forms one or more asci or spore sacs containing from two to eight ascospores. When mature the spore fruits may sometimes be seen as black specks on the leaf.

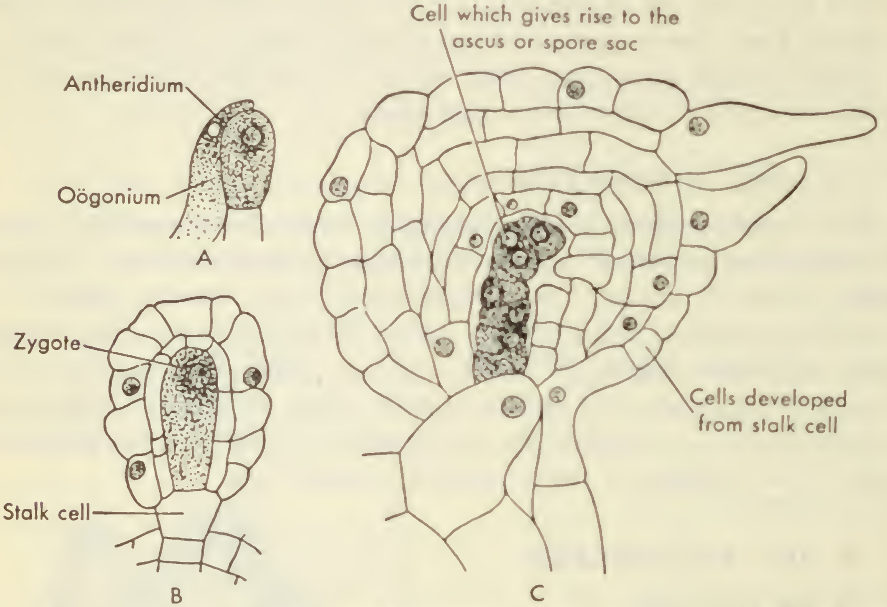

Cell which gives rise to the ascus or spore sac
Antheridium
Oögonium
A
Zygote
Stalk cell
B
C
Cells developed from stalk cell

Fig. 8:12 A powdery mildew (class Ascomycetes). Sexual reproduction and the formation of the spore fruit. A, two hyphae (one bearing an oögonium, the other an antheridium) are joining. B, the nucleus of the antheridium has passed into the oögonium and fused with its nucleus, leading to the formation of a zygote; C, the spore fruit showing the cells developed from the zygote (shaded in the figure), one of which (containing two nuclei) will give rise to the ascus and the ascospores which it contains. The other portion of the spore fruit, not shaded in the figure, is developed from the stalk cell of the hypha bearing the oögonium. Redrawn after Harper.

(3) THE BLUE AND GREEN MOLDS

Another group includes the blue and green molds. One genus, *Aspergillus,* is common on decaying vegetables, cereals, preserves, damp leather, and so forth. The characteristic green, brown, or yellow color appears when the spores develop. Another genus (*Penicillium*) occurs on bread, cheese, lemons, and other foods. One species *Penicillium natatum* (Fig. 8:13) has become famous as the source of penicillin, the production of which is referred to in the chapter on the economic and medical importance of plants. Another species (*Penicillium roqueforti*) is important in the ripening of Roquefort and Gorgonzola cheeses and still another species (*Penicillium camemberti*) is the active agent in the ripening of camembert cheese.

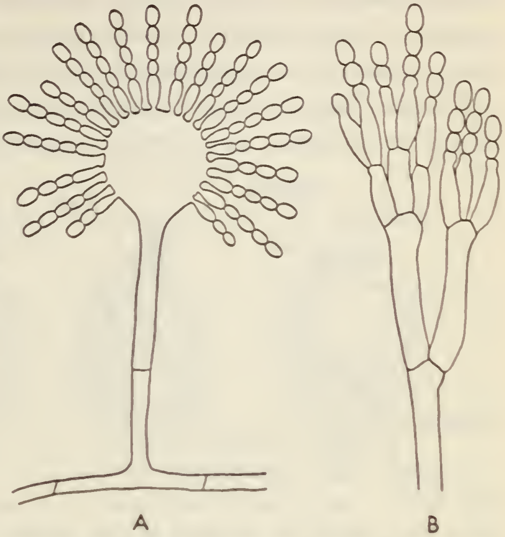


Fig. 8:13 Blue and green molds (class Ascomycetes). A, lengthwise section of a conidium-bearing branch of *Aspergillus*. B, conidium-bearing branch of *Penicillium*. Both diagrammatic. From Smith, Gilbert, *et al.*, *A Textbook of General Botany*, The Macmillan Company.

(4) ERGOT

Ergot (Claviceps) is a well-known disease of rye and other grasses. It produces large purplish-black horny grains in place of the normal seeds. The parasite attacks young flowers and grows into the ovary, replacing the ovules with its hyphae. The infected grains drop to the ground and after passing the winter produce ascospores which spread the disease.

(5) THE YEASTS

Perhaps economically the most important group of the Ascomycetes are the yeasts (genus Saccharomycetes) which are in reality degenerate forms without a true mycelium. The mysterious change of the juice of the grape into wine has been known from very ancient times. In the making of wine from grapes, grape sugar is broken down into **alcohol** and **carbon dioxide gas.** The process is called **fermentation.** The preservation of the gas in bottling causes some wines, such as champagne, to effervesce. The researches of Louis Pasteur carried on between 1860 and 1870 showed that the formation of alcohol and carbon dioxide was due to a microscopic organism calld **yeast.** Yeast is also used in the making of bread and in baking. The process of fermentation in the dough produces fine bubbles of carbon dioxide gas which cause the dough to "rise" and give to the bread its light spongy structure. For this purpose yeast is sold in the form of "yeast cakes."

If a piece of a yeast cake is crushed in a little water and examined under the microscope the very numerous yeast plants can be easily seen. These consist of single cells or small groups of cells (Fig. 8:14). The cells are either spherical or egg-shaped and each is surrounded by a well-marked cell wall. One or more vacuoles can be clearly seen in the cytoplasm. Small fat globules and irregular granules of reserve food materials are also recognizable. It is not possible to see the nucleus in the living cell but its presence can be demonstrated by special staining methods.

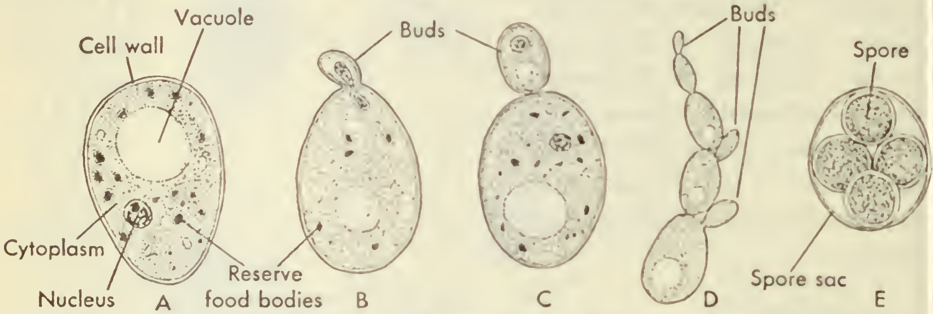


Fig. 8:14 Yeast (class Ascomycetes). A, a single cell. B–C, formation of a bud. D, the buds have remained attached to the parent cell and have themselves formed buds. E, spore formation. Redrawn after Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The yeast cell reproduces by cell division but the process is somewhat different from that in the plant cells already encountered. When cell division is about to occur a portion of the cell wall is pushed out forming a small projection or **bud.** This gradually increases in size and the nucleus divides into two portions forming two daughter nuclei one of which moves out into the bud. In budding the parent individual divides unequally so as to give rise to a smaller daughter individual. In the case of the yeast cell during active growth the buds may remain attached to the parent cell and themselves give rise to smaller buds, so that branched irregular chains of cells are formed which, however, soon break up into separate cells.

Another method of reproduction which occurs only in old cells is by the formation of spores. When a yeast cell is about to form spores the nucleus breaks up into four parts. Then the cytoplasm becomes divided by plasma membranes into four parts, each part containing one of the nuclei. The original cell wall thus comes to form a spore sac or **ascus** and each of the four cells within it becomes an **ascospore.** It is because they produce ascospores that the yeasts are classified as Ascomycetes.

Probably the most important feature of the yeast from a biological point of view is the way in which it produces fermentation. The grape sugar, called **glucose,** which is in solution in the grape juice, passes into the cytoplasm of the yeast cell through the plasma membrane and is there converted into alcohol and carbon dioxide. The alcohol and carbon dioxide pass out of the protoplast through the plasma membrane into the surrounding liquid. The yeast, which lacks chlorophyll, obtains the energy to carry on its vital activities by breaking up sugar into alcohol and carbon dioxide. If a culture of yeast is ground up in a mortar with very fine sand so as to crush and kill the individual cells the liquid will nevertheless still produce fermentation. It was at first thought that a single **enzyme,** to which the name **zymase** was given, was responsible for the fermentation caused by yeast. It has now been shown that the fermentation is due to a number of different enzymes acting in concert. It is interesting to note that our knowledge of enzymes and of many of the processes which go on in living cells in health and disease had its beginning in the study by Pasteur of the fermentation produced by yeast and other similar organisms.

C. *THE BASIDIOMYCETES*

This class includes the smuts and rusts, some of which are important parasites of economic plants, and the more familiar mushrooms and their relatives.

(1) THE SMUTS

The members of this group (order Ustilaginales) are all parasites. They may be recognized by the black sooty masses of spores which they produce on various parts of the infected plant which is usually a member of the grass family (Graminae). These black spores are scattered by the wind. When they germinate they produce short hyphae bearing small spores which are believed to be the equivalent of basidiospores. (For description of basidiospore see under "Mushrooms.") The basidiospores infect the seedlings.

(2) THE RUSTS

Certain members of this group (order Uredinales), which is composed entirely of parasitic forms, cause some of the most destructive diseases of cereals such as wheat, oats, barley, and rye. One of the best known is the wheat rust, *Puccinia graminis*. The name "rust" is due to the bright orange uredospores which when abundant give the appearance of iron rust to the infected portion of the plant (Fig. 8:15). These spores are carried in the air to new plants which they infect immediately, causing a new crop of similar spores to be formed in a few days. Later in the summer a different kind of spores, called **teleutospores,** black in color, are formed on the stem of the wheat causing a black rust. The black spores remain dormant over the winter and in the following spring send out short hyphae each of which bears four basidiospores (Fig. 8:15). (For description of basidiospore see under "Mushroom.") The basidiospores under ordinary conditions are not able to infect wheat but must reach a second host, the barberry (*Berberis vulgaris*), if they are to germinate. On the barberry a fourth kind of airborne spores is produced which must reach a wheat plant to germinate and complete the life cycle. While the life history of wheat rust usually involves two separate species of host, where the winter is mild the uredospores may survive and infect wheat in the spring.

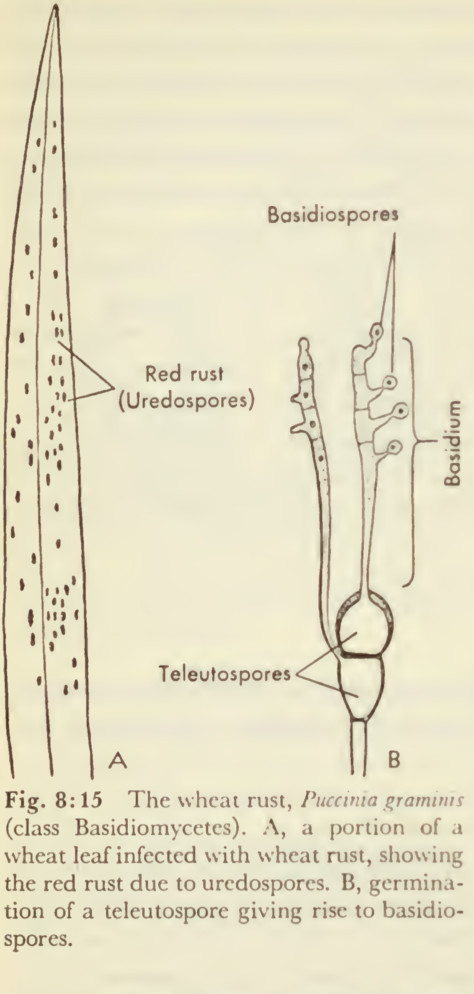


Fig. 8:15 The wheat rust, *Puccinia graminis* (class Basidiomycetes). A, a portion of a wheat leaf infected with wheat rust, showing the red rust due to uredospores. B, germination of a teleutospore giving rise to basidiospores.

(3) MUSHROOMS, PUFFBALLS, AND RELATED FUNGI

The common toadstool or visible part of a mushroom is an outgrowth from a mycelium which grows saprophytically on decaying vegetable or animal matter at the surface or just below the surface of the ground (Fig. 8:16). A single mycelium may cover a considerable area and give rise to a group of toadstools. The toadstools or mushrooms are really reproductive bodies or fructifications. This is perhaps why they grow so rapidly and give rise to a "mushroom growth." The toadstool itself is made up of a mass of interlacing hyphae. The hyphae of mushrooms, unlike those of the bread mold, are **septate,** that is, divided by cross walls. A toadstool consists of a stalk, called in this case a **stipe,** which is expanded at the top into an umbrella-shaped **cap** or **pileus.** On the under side of the cap many thin plates hang down (Fig. 8:17). These thin plates or **gills** are attached to the under side of the cap along lines which radiate from the stalk to the periphery. The surface of the gills, called the **hymenium,** is given over to the formation of spores. The ends of some of the hyphae which compose the hymenium develop into structures called **basidia.** Each basidium bears four spores called **basidiospores,** on short stalks called **sterigmata** (singular **sterigma**) (Fig. 8:17). When ripe the spores are shed. Under suitable conditions they develop into mycelia which give rise to more "mushrooms."

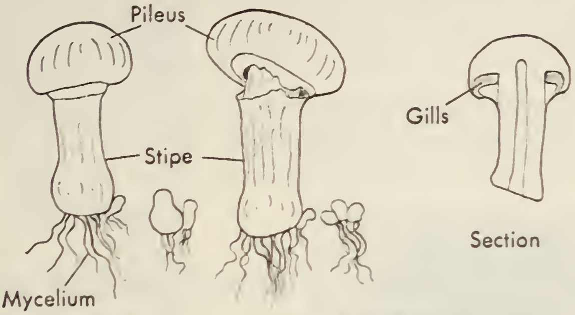


Fig. 8:16 A mushroom, *Agaricus campestris* (class Basidiomycetes). On the left, an immature fruiting body. In the center, a fruiting body approaching maturity. On the right, a longitudinal section of a fruiting body similar to that on the left.

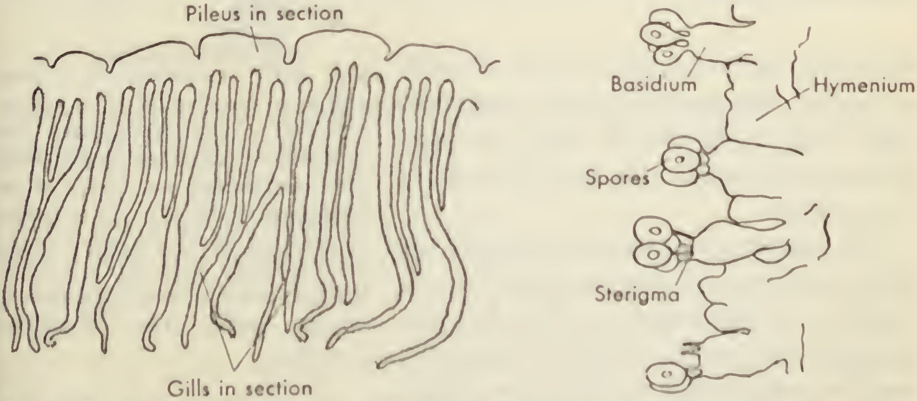


Fig. 8:17 The formation of basidiospores in a mushroom. On the left, a section of the pileus, showing gills. On the right, a part of one side of one of the gills enlarged to show the hymenium and the basidiospores.

What corresponds to fertilization in the mushroom is hidden in nuclear changes which occur preceding the formation of the basidia. As already stated, the hyphae are divided by septa into separate portions which may be called cells. However, each of these "cells" contains two nuclei.

When a basidium is formed the "cell" from which it develops also contains two nuclei. Early in the development of the basidium the two nuclei fuse forming a single nucleus. This nuclear fusion corresponds to the fusion of the nuclei of two gametes to form a zygote nucleus. The single or zygote nucleus of the basidium soon divides forming four nuclei, which become distributed one to each of the four basidiospores.

A single mushroom may produce millions of minute spores. These spores are distributed by the wind. A large number of spores is necessary in order that some may have a chance to reach the conditions required for the development of a mycelium.

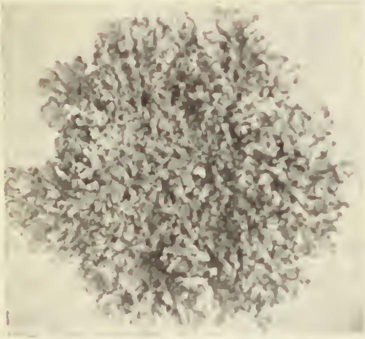


Fig. 8:18 A lichen, *Parmelia.* From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

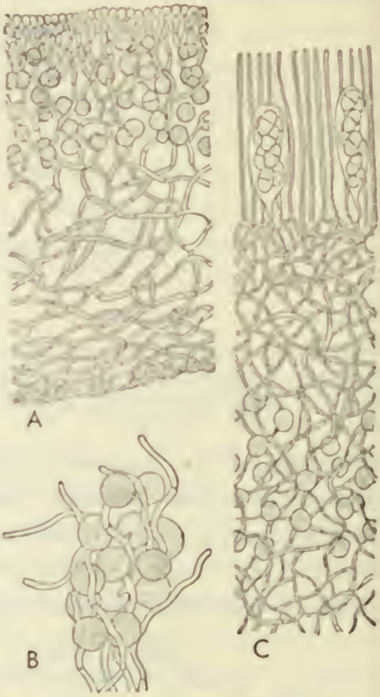


Fig. 8:19 A lichen. A, a cross section of the thallus. B, a vegetative bud containing hyphae and algal cells which, when broken away from the thallus, is capable of reproducing the lichen. C, a cross section of a portion of a lichen, showing the formation of ascospores. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The mushroom described, *Agaricus*, belongs to a group (Hymenomycetes) which includes the **gill fungi** so called because the spores are borne on gill-like filaments and the **pore fungi** in which the spore-bearing surface or hymenium lines the cavities of numerous pores opening on the under side. Most of the pore fungi occur on the trunks of trees where they form shelflike projections and are called **shelf fungi** although in a few the fruiting body takes the form of a toadstool. In **puffballs** (Gastromycetes) the spore-bearing cells are completely enclosed in the "ball" and the spores are freed either through a hole in the top or by decay of the entire fruiting body.

3. THE LICHENS

The lichens (Fig. 8:18) are an interesting group of plants which are partly Algae and partly Fungi. What appears to be the lichen plant really consists of two plants: a simple alga often resembling *Protococcus* and a fungus, the hyphae of which twine around and enclose the algae (Fig. 8:19). The relationship between the alga and the fungus is one of symbiosis. The alga is protected, held in place, and in some cases supplied with water by the fungus, while the fungus in turn receives from the alga the organic materials which it is unable to manufacture itself. The thallus of the lichen is, however, a very different structure from that of the alga or the fungus alone.

4. MODES OF LIFE ILLUSTRATED BY THE ALGAE, FUNGI, AND LICHENS

A. *INDEPENDENT AND DEPENDENT PLANTS*

The Algae are independent plants manufacturing their own food materials with energy absorbed from sunlight. The Fungi, on the other hand, with the exception of the autophytic bacteria, are all dependent plants. It is clear that among living things the independent plants must have preceded the dependent. Hence the earliest forms of life on the earth probably resembled either the autophytic bacteria or simple algae.

B. *SAPROPHYTISM*

A saprophyte has already been defined as a plant which obtains its nourishment from nonliving organic matter. The importance of such plants for maintenance of life upon the earth has been considered in connection with the carbon cycle. With a few exceptions, such as the Indian pipe which is a flowering plant, all saprophytes belong to the class Fungi. Saprophytes require to be adapted to their particular mode of life. None of them are very large plants and most of them are quite small. They grow rapidly when decaying organic material is available for them and produce an abundance of spores, since only by being widely distributed is there a chance of their reaching new sources of nourishment.

C. *PARASITISM*

A parasite has been defined as an organism which lives on or in another species of living organism from which it obtains its nourishment.

Many of the Fungi are parasites on plants or on animals. There are, however, parasitic plants which are not Fungi, such as the mistletoe and dodder, which are flowering plants. Many Fungi can live either as saprophytes or parasites. Parasitism requires even greater adaptation than saprophytism, since the parasite must be adapted to the peculiarities in the structure, physiology, and mode of life of its host or hosts. One of the most difficult problems which a parasite must solve is getting from one host to another. Hence most parasites have rather complicated life cycles and varied methods of reproduction. Sometimes more than one species of host is involved as in the wheat rust.

D. SYMBIOSIS

In the case of symbiosis two organisms belonging to different species live together to their mutual advantage. Thus in the case of the lichen, the fungus partner obtains from the alga the organic substance which it itself cannot manufacture while the alga is protected and held in place by the fungus.

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Questions

1. Outline your idea of how the thallus of such a plant as *Ulva* may have been evolved and illustrate your answer by reference to existing plants.
2. Why in general is the plant body of the Algae more finely divided and more flexible than that of land plants?
3. Discuss sex differentiation in the Algae and illustrate your answer by reference to living forms.
4. Compare the thallus of an alga with the mycelium of a fungus.
5. What reasons can you give for believing that Fungi were evolved from the Algae and not vice versa?
6. Compare the life cycles of *Spirogyra* and *Rhizopus*.
7. What methods would you advise for the combat of wheat rust?
8. What are the advantages to the individuals of the association called a lichen?
9. Distinguish between: autophytic, saprophytic, parasitic, and symbiotic modes of life.

Suggestions for Further Reading

Smith, Gilbert M., *The Fresh-water Algae of the United States*, McGraw-Hill Book Company, Inc., New York, 1933.

Gwynne-Vaughan, H. C., and B. Barnes, *Structure and Development of the Fungi*, The Macmillan Company, New York, 1922.

CHAPTER 9

Bacteria (Class Schizomycetes)

Some of the bacteria may well be considered among man's best friends, a few are his worst enemies, while many form an essential part of the vegetation of the earth. The study of bacteria forms the subject of a special science called **bacteriology**. It is possible here to touch on only the more general aspects of the subject.

Bacteria are all simple, minute organisms. They vary considerably in **size** but average about 1 μ to 3 μ in length and 0.3 μ to 0.5 μ in thickness. One of the largest is *Bacillus butschlii* which is 50 μ to 60 μ long and 4 μ to 5 μ in thickness. One of the smallest is *Bacillus influenzae* which measures 0.5 μ by 0.2 μ. Although bacteria are classified as plants it must be admitted that in the lower organisms it is difficult to make a sharp distinction between the vegetable and animal kingdoms.

Among **plant characteristics** of bacteria may be mentioned the more or less fixed and rigid shape of their cells, the tendency to grow in filaments, the ability of some (autophytic bacteria) to exist on inorganic food materials, and the fact that food materials are not ingested.

Bacteria which manufacture their own food materials from inorganic substances are said to be **autophytic.** Bacteria which occur in decaying organic matter and live by digesting and absorbing organic materials are called **saprophytic** bacteria, while to bacteria which live on or in the bodies of living organisms the term **parasitic** is applied. Parasitic bacteria may be harmless to their hosts or produce disease in them. In the former case they are said to be **nonpathogenic,** in the latter case **pathogenic.**

1. STRUCTURE

When seen in a drop of water under the microscope bacteria appear as very minute transparent spheres called **cocci** (singular, coccus); rods, called **bacilli** (singular, bacillus); spirals, called **spirilla** (singular, spirillum) or as long fine **filaments** of cells either branched or unbranched (Fig. 9:1). Without very special technique it is impossible to distinguish a cell wall or any structural differentiation within the cells. Even when stained and specially prepared for study, the entire cell may appear uniform in color. Bacteria appear to lack the definite nucleus, bounded by a nuclear membrane, which is characteristic of nearly all plant and animal cells. The place of the nucleus is taken by chromatin granules dispersed in the protoplasm. In certain species the cell is surrounded by a well-developed gelatinous envelope or **capsule** which usually fails to take up any color when the cell is stained. Another feature which serves to distinguish some species is the presence of deeply staining granules, called **polar granules,** in the ends of bacilli. Many bacteria move about under their own power. This movement is distinguished from the Brownian movement already described by being in a definite direction and not irregular. The movement is caused by extremely fine hairlike processes called **flagella.** There may be a single flagellum attached to one end of the cell, two or more at either or both ends, or they may be distributed over the cell. Although the movement which they produce is readily visible the flagella themselves are invisible except by the use of special techniques.

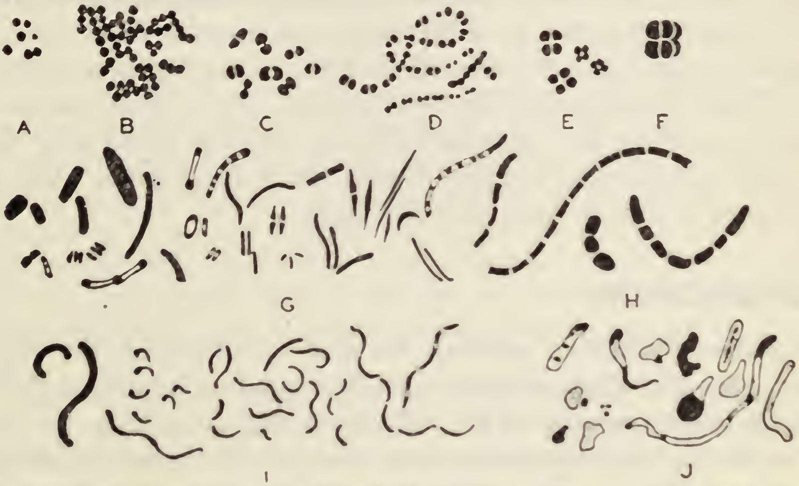

Fig. 9:1 Forms of the Lower Bacteria. A, cocci; B, staphylococci; C, diplococci; D, streptococci; E, tetrads, groups of four cocci; F, sarcinae; G, bacilli, various forms; H, streptobacilli; I, spirilla, various forms; J, involution forms. Reproduced from Kenneth L. Burdon, *A Textbook of Microbiology*, The Macmillan Company.

Bacteria multiply only by cell division which in this case is called simple **fission.** In the case of cocci after division the cells may adhere together in pairs when the organism is called a **diplococcus** or in irregular groups when it is called a **staphylococcus** or in chainlike filaments when it is called a **streptococcus** or in cubes when it is called a **sarcina.** Bacilli may adhere in pairs forming **diplobacilli** or in chains forming **streptobacilli.** Spirilla usually occur as single cells but they may form long wavy chains.

When bacteria are grown under unfavorable conditions, as often happens in old cultures, they may become swollen or shrunken and take on unusual shapes. Bacilli and spirilla may become long tangled filaments. In such cases the bacteria are referred to as **involution forms** (Fig. 9:1).

Certain species of bacilli are able to form resistant **spores** when conditions become unfavorable for their growth. This process consists of a condensation of the cell contents into a spherical or ovoid body with a thick wall, each bacillus being converted into a single spore. Such spores are resistant to drying, heat, and chemicals.

2. CLASSIFICATION

A number of different methods are used to distinguish the different kinds of bacteria. These methods include the determination of the morphological characteristics of the individual and the colony, the occurrence of the bacterium in nature, the way in which it takes up biological stains, the conditions under which it can be grown or cultivated, including the requirements in food materials and temperature and whether it will grow in the presence or absence of oxygen, the chemical changes which it produces, and the pathological changes (if any) which it causes. In the early days of bacteriology only a few generic names such as *Coccus*, *Bacillus*, and *Spirillum* were used. Now with newer techniques bacteriologists distinguish over one hundred different genera. This has resulted in the substitution of many new names for the old ones and considerable confusion in the nomenclature.

A detailed classification of the bacteria is beyond the scope of this book. The following is an abbreviated classification which emphasizes the general relations of the group.

Classification of the Bacteria (Class Schizomycetes)[1]

LOWER BACTERIA (Order Eubacteriales). The cell takes the form of a sphere or rod, either straight or curved.

Family Nitrobacteriaceae. Nearly all are rod-shaped and live in water or soil and not as parasites. They are able to derive their energy from the oxidation of carbon, hydrogen, sulphur, or nitrogen, or simple compounds of these. Examples: *Nitrosomonas*, *Azotobacter*, both soil bacteria.

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[1] Simplified from Tanner, F. W., *Bacteriology*, John Wiley & Sons, Inc., New York, 1937.

Family Coccaceae. Spherical forms which may divide in one, two, or three planes. Cells may adhere in pairs (*Diplococcus*), in irregular groups (*Staphylococcus*), or in chains (*Streptococcus*). Usually nonmotile and without spore formation. Energy usually obtained from amino acids or carbohydrates. Many are parasitic and some are pathogenic. Examples: *Diplococcus* (*Pneumococcus*)[1] *pneumoniae*, the cause of lobar pneumonia; *Streptococcus; Neisseria* (*Gonococcus*) *gonorrhoeae*, cause of gonorrhea; *Neisseria* (*Meningococcus*) *intracellularis*, cause of epidemic meningitis.

Family Spirillaceae. Cells elongated and spirally curved. Cell division transverse. No spores formed. Move by means of flagella at one end. Most occur in water but some are intestinal parasites. Example: *Vibrio comma* (*Microspirillum choloreae*, *Spirillum choloreae*), cause of Asiatic cholera.

Family Bacteriaceae. Rod-shaped bacteria. Energy usually obtained from amino acids and carbohydrates. Many are soil or water bacteria and produce fermentation. Some are parasites. Examples: *Escherichi* (*Bacillus*) *coli*, the harmless bacillus of the intestine; *Eberthella typhosa* (*Bacillus typhosus*), cause of typhoid fever; *Salmonella* (*Bacillus*) *paratyphi* and *Salmonella* (*Bacillus*) *schottmuleri*, cause of the plague and *Hemophilus* (*Bacillus*) *pertussis*, cause of the whooping cough.

Family Bacillaceae. Rod-shaped forms often forming long chains. Saprophytes or parasites. Examples: *Bacillus subtilis*, a large bacillus frequently found in hay infusions; *Clostridium* (*Bacillus*) *tetani*, cause of tetanus.

HIGHER BACTERIA

Moldlike bacteria (Order Actinomycetales). Cells elongate, frequently filamentous and sometimes branching. Examples: *Mycobacterium* (*Bacillus*) *tuberculosis*, cause of tuberculosis; *Corynebacterium* (*Bacillus*) *diphtheriae*, cause of diphtheria.

Sheathed bacteria (Order Chlamydobacteriales). Filaments of cells with sheaths which frequently become impregnated with iron oxide. Example: *Cladothrix*, an iron bacterium.

Sulphur bacteria (Order Thiobacteriales). Cells typically contain granules of sulphur and grow best in the presence of hydrogen sulphide. Example: *Thiothrix*, a sulphur bacterium.

Spirochaetes (Order Spirochaetales). Protozoalike bacteria. Cell takes the form of a long thin spiral with a wavy motion. Cell division is longitudinal. Example: *Treponema pallidum*, the cause of syphilis.

3. CULTIVATION

In studying bacteria it is usually not enough simply to examine a small quantity of soil or water or mucus under the microscope. A special technique is necessary to discover the conditions under which the species grows and the effects which it produces.

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[1] Parentheses indicate synonyms

Suppose, for example, it is desired to study some of the species of bacteria which live in the water in a particular well. The first thing to be done is to obtain a sample of the water uncontaminated with bacteria from other sources. This can be done by taking the sample in a stoppered bottle which has been previously **sterilized**. The stoppered bottle is sterilized by heating it in an oven to a temperature of 170° C for an hour. This kills all bacteria which may be present.

The next step is to grow or cultivate the organisms without contamination. For this purpose a sterile **culture medium** is used which varies with the type of organism being studied. In water analysis cultures are usually made on nutrient agar [1] or gelatin, containing beef extract and peptone. This medium is liquid when heated but solidifies to a stiff jelly when cooled. The culture medium is placed in a flask or test tube closed with a stopper of nonabsorbent cotton and sterilized in an apparatus called an **autoclave** (Fig. 9:2). This apparatus is very similar to the household steam sterilizers used in the canning of fruits. In such an apparatus on account of the pressure generated the temperature of the culture medium can be raised considerably above that at which it would boil at atmospheric pressure. A pressure of 15 to 20 pounds per square inch, which corresponds to a temperature of 121° to 126° C, is usually used and maintained for a period of 20 minutes to half an hour. The nonabsorbent cotton stoppers serve to exclude bacteria while at the same time admitting an interchange of gases and the equalization of the pressure inside and outside the flask or test tube. While still hot the nutrient agar or gelatin is poured into sterilized flat glass dishes with covers called Petri dishes. There, on cooling, it forms a transparent layer on the bottom of the dish which can be examined with a magnifying glass or even the low power of the compound microscope.

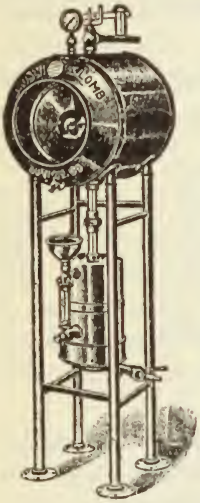
Fig. 9:2 An autoclave such as is used for sterilizing culture media and instruments. From Buchanan and Buchanan, *Bacteriology*, The Macmillan Company.

The bacteria in the water sample must now be transferred to the nutrient agar or gelatin in the Petri dishes. A small quantity of the water is taken from the bottle in a sterile pipette and distributed over the agar. Usually a number of different Petri dishes are used and different quantities of water taken from the sample. If the object is to examine the water for the possible presence of pathogenic organisms, the Petri dishes are placed in an incubator which is customarily kept at 37° C (98.6° F), the temperature of the human body, for about two days. At this time some of the plates will usually show numerous small **colonies** of bacteria, which appear to the naked eye or under the hand lens as little round patches on the transparent agar or gelatin (Fig. 9:3).

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[1] A substance obtained from a seaweed which forms a stiff jelly.

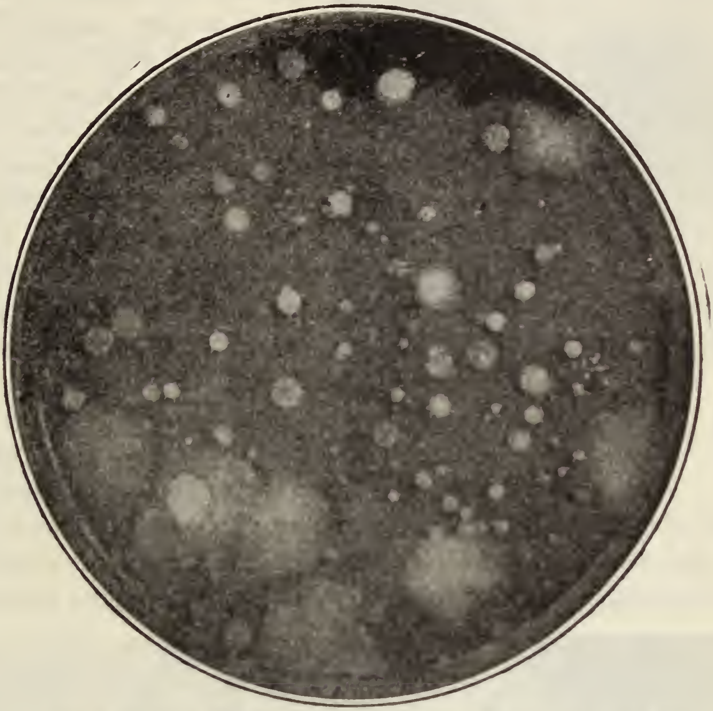

Fig. 9:3 Culture of bacteria. A Petri dish showing the isolated colonies from which pure cultures may be secured. From Buchanan and Buchanan, *Bacteriology*, The Macmillan Company.

For further study it is best to choose a Petri dish in which the colonies are not so numerous as to touch one another. The different colonies can be examined under the microscope and their characteristics recorded (Fig. 9:4). It is evident that each colony has arisen from a single bacterium or possibly a clump of bacteria. In the first case it is clear that the bacteria in the colony will all be of the same species.

The method outlined above for obtaining cultures of bacteria from water also provides a method of estimating the number of bacteria per cubic centimeter of water in the sample which will grow under the conditions provided in the Petri dish. It is only necessary to measure the exact amount of water added to the Petri dish and to count the number of colonies on the agar or gelatin in the dish. A simple calculation then gives the number per cubic centimeter in the sample. If it is now desired to study the bacteria of one of the colonies in further detail a pure culture, i.e., one containing only a single species of bacterium, may be obtained by transferring a few bacteria from one of the colonies on the tip of a sterilized needle to another Petri dish or test tube containing fresh sterile culture medium, taking precautions to prevent contamination (Fig. 9:5). The culture so obtained would be called a **pure culture** if the bacteria which it contained all belonged to the same species.

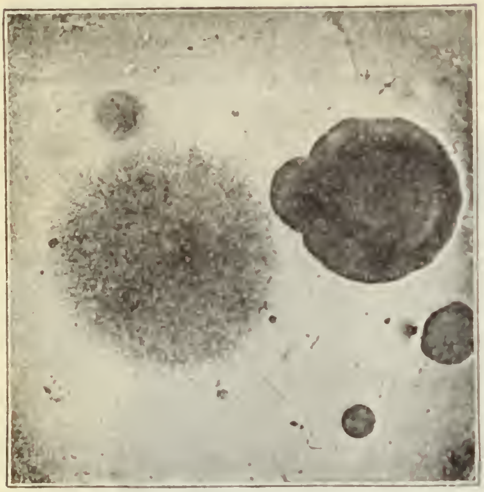

Fig. 9:4 Bacterial colonies on an agar plate. Magnified × 20. From Buchanan and Buchanan, *Bacteriology*, The Macmillan Company.

Similar methods are applied to the study of bacteria in milk, soil, sewage, and so on, modified in each case to suit the material from which the sample is to be taken and the kinds of bacteria which are to be studied.

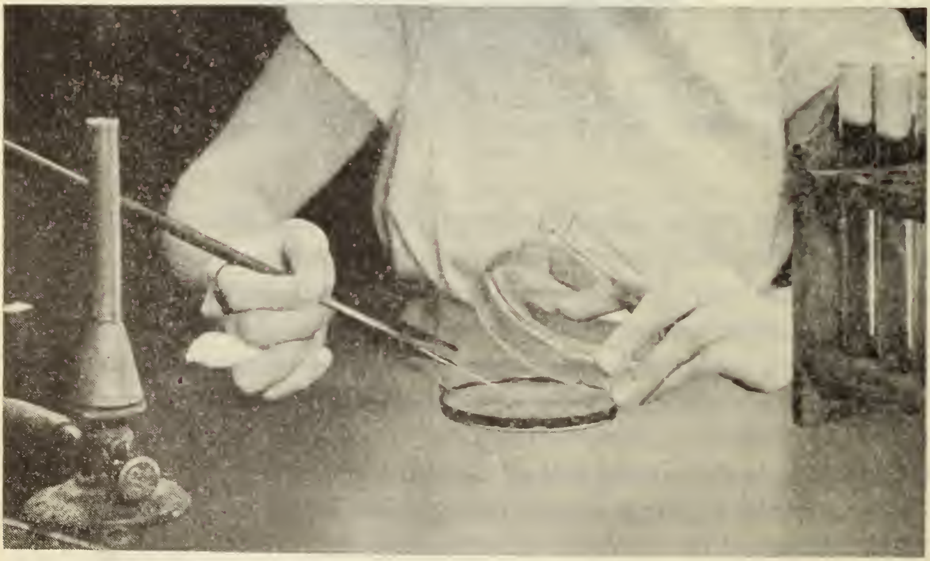

Fig. 9:5 Subculturing bacteria to isolate desired strains. Transfer of bacterial colonies from Petri dish to test tube containing sterile culture media. Photograph by the Parke Davis Company.

4. CHEMICAL ACTIVITIES

By using a culture medium of known chemical composition and cultivating in it bacteria of a single species it is possible to investigate the chemical changes which the bacteria bring about in it. As in the case of the yeast it is also possible to show that the changes are usually promoted by enzymes.

Like all living things bacteria respire, i.e., oxidize food materials to obtain energy. Bacteria which use the free oxygen of the atmosphere or oxygen dissolved in their liquid environment are called **aerobes** (Gr. *aer*, *aeros*, air + *bios*, life). On the other hand there are many species of bacteria which do not require free oxygen and are able to obtain oxygen for their respiration from oxygen compounds. This occurs in the case of bacteria (and also yeast) which decompose glucose to form alcohol and carbon dioxide.

$$\underset{\text{Glucose}}{C_6H_{12}O_6} = 2\ \underset{\text{Ethyl alcohol}}{C_2H_5OH} + 2\ CO_2$$

The amount of energy available from this type of respiration is much less than when free oxygen is used. This is because the glucose molecule is not completely oxidized and much of the energy stored in it remains in the alcohol. Organisms which do not require free oxygen for their respiration but can nevertheless exist in the presence of free oxygen and utilize it for their respiration are called **facultative anaerobes** (Gr. *an*, without). There are a few organisms which not only do not require free oxygen but are actually poisoned by it so that they will grow only in the absence of free oxygen. Such organisms are called *anaerobes*.

Bacteria are frequently active in breaking down organic compounds. Two terms have been used in describing their action, fermentation and putrefaction. **Fermentation**[1] may be defined as the decomposition of carbohydrates by living cells. A typical case is that of the **fermentation of sugar** by yeast. Certain species of bacteria are able to ferment monosaccharides and disaccharides. The reaction may be represented as

$$C_6H_{12}O_6 + 6\ O_2 \longrightarrow 6\ CO_2 + 6\ H_2O$$

The word "fermentation" comes from a Latin word meaning "to boil" and refers to the bubbling due to the carbon dioxide given off. However, fermentation may occur without the evolution of carbon dioxide; in place of it an organic acid may be formed as in the **souring of milk** when the sugar lactose is changed to lactic acid. Two steps are involved. First the lactose is hydrolyzed to monosaccharides and then the monosaccharides are changed to lactic acid.

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[1] Some ambiguity attaches to the use of this term which is sometimes given a much wider meaning which would include putrefaction.

First step: $\underset{\text{Lactose}}{C_{12}H_{22}O_{11}} + H_2O \longrightarrow \underset{\text{Glucose}}{C_6H_{12}O_6} + \underset{\text{Galactose}}{C_6H_{12}O_6}$

Second step: $\underset{\text{Glucose or Galactose}}{C_6H_{12}O_6} \longrightarrow \underset{\text{Lactic acid}}{2\ C_3H_6O_3}$

The bacteria concerned in this fermentation are called **lactic acid bacteria.** They are usually facultative anaerobes.

Putrefaction is the decomposition of proteins and the products of protein breakdown. The earlier stages in the putrefaction of proteins usually take place in the absence of oxygen and when they are due to bacteria, the bacteria are usually anaerobes. In these stages the proteins may be reduced to proteoses, peptones, peptids, and amino acids by hydrolysis (see Chap. 6, Art. 1). Some of these substances have foul odors evident in the bad smells usually present during the early stages. The later stages usually require oxygen and when caused by bacteria, the bacteria are usually aerobic. The amino acids are deaminized, i.e., the amino group, NH_2, is separated off as ammonia, NH_3, and decarboxylized, i.e., the carboxyl group, COOH, is separated and carbon dioxide, CO_2, is given off. Some of the products of the decomposition of proteins are poisonous. Among them are the substances called ptomaines. However, so-called ptomaine poisoning or acute indigestion from eating putrefied food is usually due not to the ptomaines but to bacteria taken into the intestine with them. A few species of bacteria are able to decompose fats into glycerin and fatty acids. Some bacteria form highly colored colonies in culture dishes or tubes.

Most pathogenic bacteria produce poisonous substances called **toxins.** Some species, for example *Corynebacterium* (*Bacillus*) *diphtheriae*, the cause of diphtheria, and *Streptococcus scarlatinae*, the cause of scarlet fever, excrete the toxin from their cell bodies. In this case the toxin is called an **exotoxin.** In other species, for example *Eberthella* (*Bacillus*) *typhosus*, the cause of typhoid fever, the toxin is not released until after the death of the bacteria and is then called an **endotoxin.**

5. BACTERIA IN THE SOIL

One of the most important activities of bacteria is the making of nitrogen available for other plants.

Although **nitrogen** is the most abundant gas in the atmosphere and is found in combination in a large number of substances in nature the nitrogen available in the soil for plant growth would soon be exhausted if it were not replenished. Nitrogen is returned to the soil mainly by the decay and decomposition of the bodies of the plants and animals. Decay and decomposition are brought about by many different kinds of bacteria and other fungi. In most cases the decay leads eventually to the formation of **ammonium compounds.** A few plants, including many of the common cereals (order Graminales), can use ammonium compounds as a source of nitrogen but most green plants require **nitrates** (e.g., KNO_3). For these latter plants the nitrogen is made available by nitrifying bacteria which form nitrates from the ammonium compounds. Nitrogen is also added to the soil by bacteria, called nitrogen-fixing bacteria, which are able to take nitrogen from the atmosphere and bring it into combination.

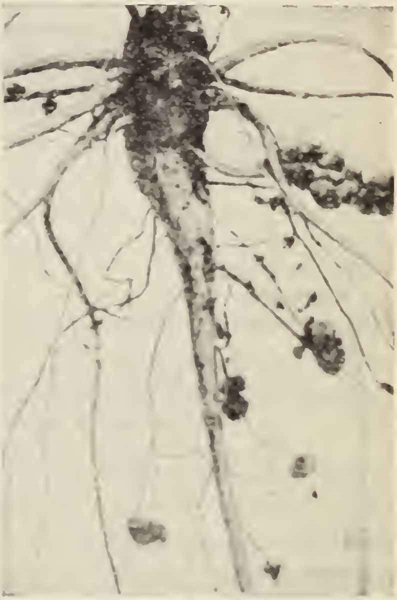

Fig. 9:6 Roots of a plant of the scarlet runner bean (*Phaseolus multiflorus*) showing tubercles which contain symbiotic nitrogen-fixing bacteria. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

The formation of nitrates from ammonium compounds in the soil by **nitrifying bacteria** takes place in two steps. The formation of **nitrites** (e.g., KNO_2) from ammonium compounds which is an oxidative process is brought about by bacteria of the genus *Nitrosomonas* (order Nitro-bacteriaceae). The nitrites so produced are further oxidized to form nitrates by another genus, *Nitrobacter*. *Nitrosomonas* and *Nitrobacter* obtain the energy to carry on their vital functions from these oxidations and at the same time supply nitrates for the use of other plants. They cannot carry on their activities in a soil which is deficient in oxygen.

Nitrogen-fixing bacteria occur free in the soil and in association with higher plants. *Azotobacter* lives in the soil. It takes free gaseous nitrogen from the atmosphere and combines it with other elements to form nitrogen compounds. This, however, requires energy. The energy is obtained from the oxidation of decaying organic material. A different mode of life is illustrated by *Rhizobium*, another nitrogen-fixing bacterium, which lives in small nodules or tubercles in the roots of such plants as the clover, pea, bean, and others, belonging to the family Leguminosae of the order Rosales (Fig. 9:6). These bacteria enter into partnership with the plant, giving it nitrogen compounds and receiving in return organic food materials. The association is an excellent example of symbiosis. **Leguminous plants,** such as clover, add nitrogen compounds to the soil and so are often grown and "plowed in" on land that has been depleted of its nitrogen by other plants. This practice has long been carried on by farmers as a step in the **rotation of crops.**

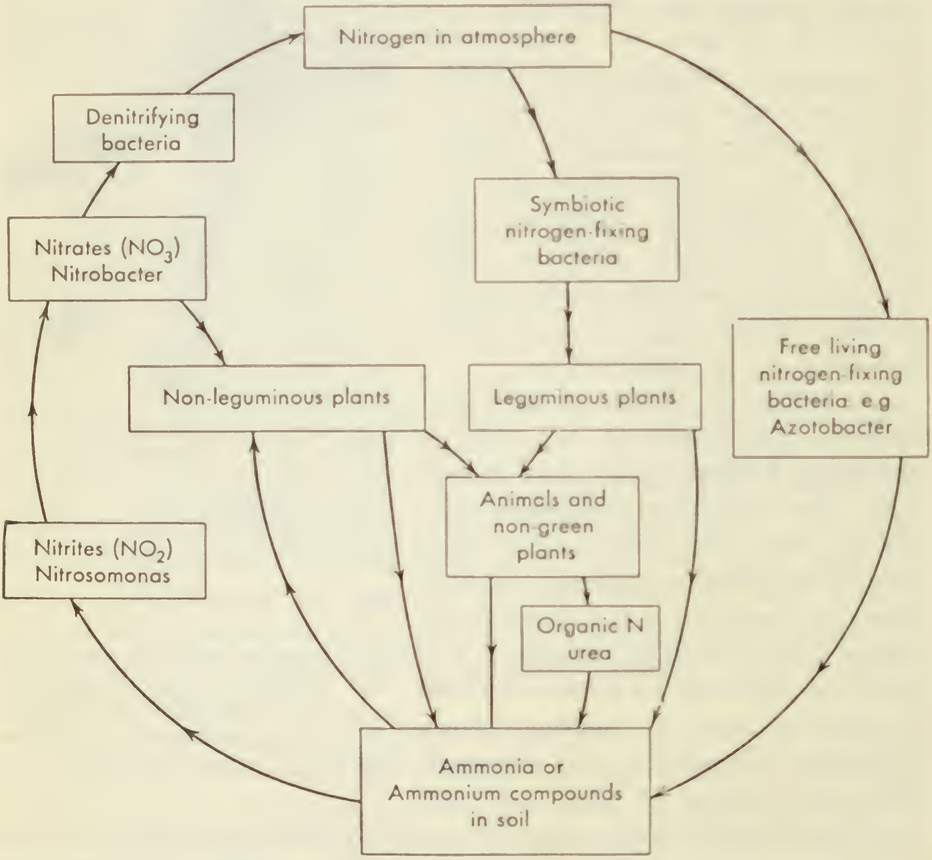
Nitrogen in atmosphere
Denitrifying bacteria
Symbiotic nitrogen-fixing bacteria
Nitrates (NO_3) Nitrobacter
Free living nitrogen-fixing bacteria e.g. Azotobacter
Non-leguminous plants
Leguminous plants
Animals and non-green plants
Nitrites (NO_2) Nitrosomonas
Organic N urea
Ammonia or Ammonium compounds in soil

Fig. 9:7 The nitrogen cycle.

Sometimes the soil may contain an excess of nitrogen compounds. Such a condition is favorable for still another group of soil bacteria, the **denitrifying bacteria.** These reverse the action of the nitrifying bacteria changing nitrates to nitrites and nitrites to ammonium compounds or to free nitrogen. In the latter case the nitrogen passes into the atmosphere and is lost from the soil. Denitrifying bacteria may also become active when the soil is deficient in oxygen.

There is a nitrogen cycle (Fig. 9:7) just as there is a carbon cycle. The cycle may include the free nitrogen of the atmosphere or, as is more usually the case, the nitrogen may pass only from one compound to another. Beginning, however, with the nitrogen of the atmosphere this may be "fixed" by bacteria either of the *Azotobacter* type which live free in soil or by bacteria of the *Rhizobium* type in the roots of leguminous plants. In the latter case the nitrogen becomes immediately available to the leguminous plants and through them to animals. In any case with the death and decay of the organisms the proteins or other nitrogenous compounds are decomposed by the bacteria of decay and finally appear in the soil as ammonium compounds. The nitrifying bacteria then change these, forming first nitrites and then nitrates. It is these nitrates which are the main source of supply for the plant world and through it for the animal world. A portion, probably always relatively small, of these nitrates may be decomposed by *denitrifying bacteria* and nitrogen freed into the atmosphere.

Sulphur is essential to all organisms and may be said to have a "cycle." The foul-smelling gas, hydrogen sulphide, H_2S, which is a product of organic decay is changed to sulphur and finally to sulphuric acid, H_2SO_4, by **sulphur bacteria** (order Thiobacteriales).

From the point of view of the origin of life upon the earth the nitrifying bacteria and the sulphur bacteria have an especial interest. They are able to carry on their living processes, including the manufacture and the utilization of food materials, without the presence of other organic matter or of light. They obtain the energy from oxidations, oxidizing ammonia, nitrites, hydrogen sulphide, or sulphur, chemical reactions which yield energy. This energy is used to build up organic food substances. These bacteria thus make use of chemical energy while green plants utilize the energy of light. This method of food manufacture is called **chemosynthesis.**

To the list of soil bacteria must be added those spore-forming parasitic forms which may be there. These include the spores of the bacteria which cause tetanus (lockjaw) and gas gangrene of wounds (prevalent in the First World War). The spores of a bacterium which give rise to the food poisoning known as **botulism** also occur in the soil.

6. BACTERIA IN WATER

A drop of rain water starting from a cloud high above the surface of the earth may be in the beginning free from bacteria. As it drops through the atmosphere it is likely to collect dust and the spores of bacteria and become no longer sterile. Bacteria are unable to grow and multiply in chemically pure water, such as that obtained by careful distillation, but they may survive there for a time. Bacteria become abundant in water only when it contains decaying or decayed organic material. Such material is added to water as it flows through or over the soil. The purity of a mountain stream is proverbial while the contamination of a muddy river is taken for granted. Many species of bacteria have their natural home in the water of ponds, rivers, and lakes. Here they perform a useful service similar to that performed by the bacteria of the soil, causing decay and reducing higher organic materials to simpler substances available for plant and animal life.

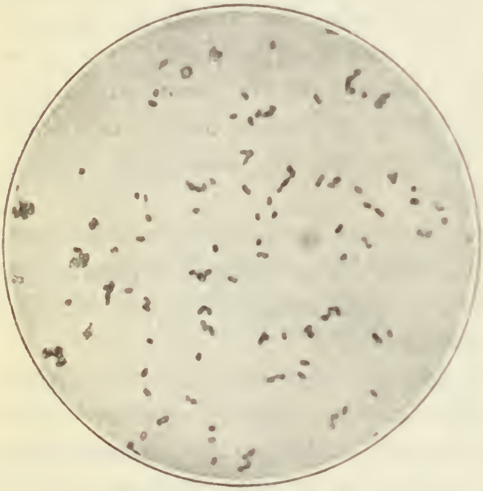

Fig. 9:8 *Bacterium coli.* From Buchanan and Buchanan, *Bacteriology*, The Macmillan Company.

On account of the necessity of water as a food for man and animals and the fact that sewage may and often does find its way into most bodies of water, great importance is attached to the relation between sewage and sources of water supply. The intestines of most animals, and man is no exception, harbor vast numbers of bacteria. Indeed, the feces of some animals are composed almost entirely of bacteria. Many of the forms are useful in helping to break down and digest materials in the digestive tract, others may cause disease. Chief among the diseases caused by intestinal bacteria and transmitted through drinking water are **cholera, typhoid fever,** and many forms of **dysentery.**

The disposal of sewage is a very necessary and important matter. The usual method of disposing of the wastes from the kitchen and bathroom is to pass them into some near-by body of water. If this body of water is also the source of the kitchen supply an excellent path for infection is laid down. The method by which a sample of water may be tested for its bacterial content has already been outlined in a previous section.

The object of the **bacteriological analysis of water** is to guard against water-borne infectious diseases. Although the bacteria which cause cholera, typhoid fever, and certain kinds of dysentery are well known and can be obtained in pure cultures, and although there is abundant evidence from other sources that the contamination of water, milk, or oysters with these bacteria may cause epidemics, it has usually proved extremely difficult or impossible to isolate the bacteria from the water supply. The bacteriologist is, therefore, usually content with a search for evidences of contamination with other and more abundant intestinal bacteria, usually the colon bacillus (Fig. 9:8), the presence of which enables him to report a contamination with sewage.

Modern methods of **sewage disposal** utilize bacteria to promote decay and ultimately purify the water. The sewage disposal plants of most of our large cities are in reality bacteriological gardens where the bacteria of decay are cultivated on a large scale. After the coarser, insoluble materials (sticks, china, bones, and so on) have been removed by passage through a strainer, the sewage arrives in large sedimentation tanks where the bacteria of decay begin their work and the solid matter sinks to the bottom forming sludge. So far **aerobic bacteria** which grow best in the presence of oxygen have been encouraged. Now other bacteria are called into play. From the surface of the sedimentation tank the water may pass to septic tanks from which air is excluded to give the **anaerobic bacteria** which flourish in the absence of oxygen, full play. Then it may

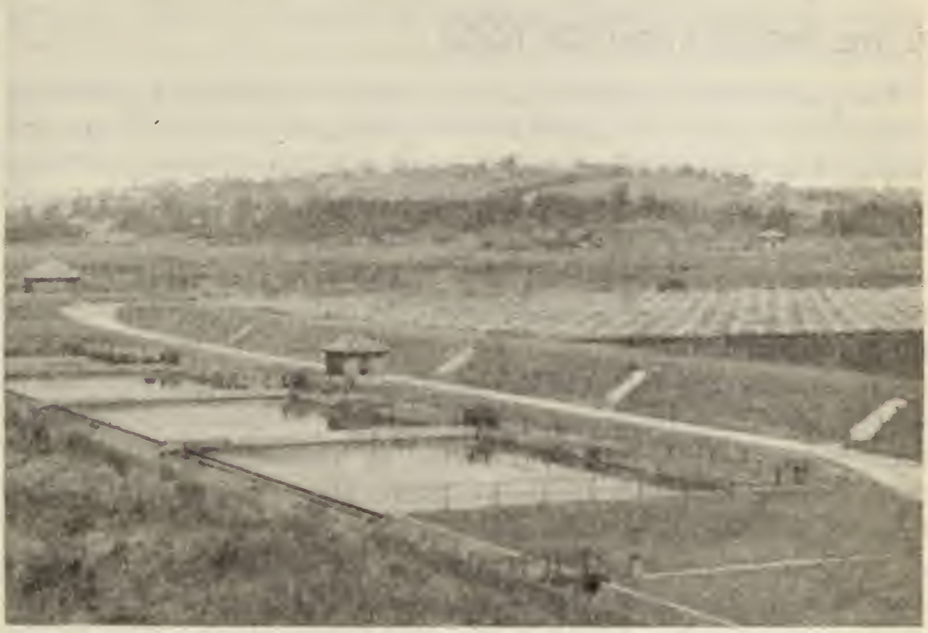

Fig. 9:9 A modern sewage disposal plant. The sedimentation tanks where aerobic bacteria are at work are in the left foreground. The septic tanks where anaerobic bacteria are encouraged are underground slightly above and to the right of the open tanks. Beyond the septic tanks and to the right of them are the filter beds on to which the liquid from the septic tanks is being sprayed through thousands of small nozzles. Photograph by J. W. Mavor.

be squirted through the air on to filter beds composed of small pieces of stone coated with slime where aerobic bacteria in the presence of oxygen reduce the remaining organic matter to ammonia or ammonium salts (Fig. 9:9). After this thorough and lengthy process the water may be free from injurious bacteria. However, if it is to pass into a source of water supply it is usually **chlorinated,** i.e., treated with gaseous or liquid chlorine.

7. THE PRESERVATION OF FOOD

The preservation of food materials is largely a problem of preventing the growth in them of bacteria or other organisms of decay (yeasts and molds). The methods in use may be classified in three groups: first, those in which the organisms of decay are killed by heat and the access of more organisms prevented; second, those in which the growth of such organisms as may be present is prevented or much retarded by cold; and third, those in which chemical substances are added to retard the growth of or kill the bacteria.

The first method involves the **sterilization** of the material and its storage in sterile, air-tight or at least dust-tight containers. Food which is not injured by heat may be preserved **by heating** it in a sealed container until all microorganisms are killed. This is the method used in canning factories where the sealed can is heated to 110° to 120° C for 20 to 30 minutes or longer depending on the size of the can. Canned food may go bad either through defective sealing of the can, which allows access of organisms, or through insufficient heating. Many of the bacteria which cause the fermentation of canned foods give off gas which may accumulate in sufficient quantity to bulge or even burst the can. The development of such organisms in a can renders the food which it contains unfit for consumption. Where heating to the temperature of boiling water or higher makes the material unpalatable or otherwise less suitable for food, **pasteurization** (named after Louis Pasteur) may be used. The exact procedure in pasteurization depends on the material to be pasteurized and the organisms to be guarded against. **Milk** may be pasteurized by heating in a closed vessel to a temperature of 60° to 70° C for 20 to 30 minutes or a temperature of 80° to 85° C for 1 minute. This treatment is effective in killing bacteria which do not form spores.

In the second method growth may be prevented or greatly reduced by a low temperature. In the preservation of food by **cold storage,** the microorganisms are not killed but simply inhibited from developing, owing to the temperature. When returned to room temperature food preserved in this way tends to decay even more rapidly than fresh food. A temperature near the freezing point is necessary to preserve most foods for any length of time. Even at such temperatures most animal foods including meats, eggs, and fish undergo a slow process of decay; for this reason meats and fish are often frozen.

In the third method **preservative substances** are added. Some of these substances are quite harmless such as sugar and salt which act by increasing the osmotic pressure and plasmolyzing the cells of the decay organism. The use of poisons in preserving foods is not to be recommended as they may exercise the same harmful effect on the organism eating the food as they do on the decay organism. In certain cases the products of fermentation prevent further bacterial or other growth and are nevertheless not injurious when taken into the digestive tract. This is the case with sauerkraut and dill pickles.

Ptomaines are produced by certain microorganisms when growing in the absence of oxygen. They result from the changing of an amino acid into an amine. Some are highly poisonous. While ptomaines may be produced in contaminated canned food where the conditions are often favorable for the growth of the microorganisms which produce them, as stated under "Putrefaction," most cases of so-called ptomaine poisoning are due either to infection with pathogenic bacteria or to bacterial poisons (toxins).

8. BACTERIA IN INDUSTRY

In industry bacteria have two very different and important roles which may be likened to those of the hero and the villain in a play. The role of the villain has already been described in the precautions necessary to preserve food; the role of the hero is played in the manufacture of food substances and other useful materials.

In many of their activities bacteria resemble the yeast plant. Although the yeasts do not belong to the same group of organisms as the bacteria, it is convenient to refer to them again here on account of their industrial importance and the similarity between the chemical changes which they bring about and those caused by bacteria. How the yeast plant causes fermentation, in this case the breaking down of sugar into alcohol and carbon dioxide, has been briefly outlined in Chap. 7.

Comparatively few species of bacteria are capable of producing **alcoholic fermentation** and none are of economic importance in this respect. In making beers, wines, and other alcoholic beverages yeasts are used. Bacteria are, however, of importance in causing the **spoiling**

of wines. This can be prevented by the pasteurization of the grape juice or other material to be fermented and then inoculating it with a pure culture of yeast.

A number of different bacteria are used in making **vinegar** from cider, wines, and certain other alcoholic solutions. The bacteria grow in a film on the surface of the liquid and are active only in the presence of oxygen. By their action the alcohol is oxidized to form acetic acid which is the main constituent of vinegar. Bacteria are used in the fermentation of cornstarch to produce **butyl alcohol** and **acetone,** organic solvents having many important uses in industry.

The **souring of milk** is a form of fermentation and is due to the formation of lactic acid from the sugar in the milk by certain species of bacteria. The ripening of cream preparatory to churning in making butter is in reality a souring process. In creameries the cream is usually pasteurized and inoculated with a pure culture of lactic acid bacteria. Bacteria also are an important factor in the manufacture of **cheese.**

Other industries in which bacteria play an important part are in the preparation of coffee and cocoa where they are used to digest the covering of the seeds, and in the tobacco industry where they are used for curing the leaves. The digestive action of bacteria is also employed in the textile industry. Here bacteria are used in retting or separating the fibers of hemp and flax preparatory to spinning. The process of tanning hides in leathermaking involves the use of bacteria.

9. BACTERIA AND DISEASE

A. *BACTERIA AS A CAUSE OF DISEASE*

Many theories have been held as to the nature and cause of disease. Most savage and primitive peoples today, and the same was probably true of early man, connect disease with magic and religion. Accordingly they believe that disease is due either to the entrance of evil spirits into the body (**demonic theory**) or to the displeasure of the gods above and their punishment of man (**punitive theory**). The Greek physician, Hippocrates (460 B.C.), called "the father of medicine," expounded the theory (**humoral theory**) that four humors or liquids held sway over the body, blood, phlegm (mucus), yellow bile, and black bile. In health these humors were present in certain proper proportions. When any one of them exceeded its proper proportion disease resulted. This theory found its expression in bloodletting and persists up to the present time in certain countries where leeches are still used. The old name for a doctor was "leech." The modern theory of the cause and nature of infectious diseases may be called the **germ theory.** Although some of the early writers and investigators suggested that infectious diseases might be caused by organisms, the modern theory and to a large extent the modern methods of combating disease may be said to have grown out of the work of Pasteur and Koch.

Louis Pasteur (1822–1895) started his scientific career as a chemist investigating the forms of **tartaric acid**, an organic compound which occurs as a precipitate in wine vats. Tartaric acid exists in two isomeres identical except for the fact that one of them rotates the plane of polarized light to the right, the other to the left. Using the sodium ammonium salt of the acid, Pasteur was able to show that the crystals of the **isomeres,** which were asymmetrical, were mirror images and thus to lay the foundation for the explanation of optical isomerism in terms of molecular structure. Pasteur further found that while one of the isomeres was fermented by a species of mold, *Penicillium glaucum*, the other was not. This seems to have led him to the study of fermentation and the investigation of spontaneous generation, then a matter of scientific controversy. Pasteur did much to prove that **fermentation** does not occur without the introduction of organisms and at the same time showed that the so-called diseases of wines, vinegar, and beer, which are due to fermentation, can be stopped by heating to 55° to 60° C — a method which is now called **pasteurization** and applied extensively to milk.

At the invitation of the French government Pasteur turned from his investigations of fermentation to work upon a **silkworm disease** known as pebrine, which threatened to ruin the silk industry. With singular success he was able to discover the cause of the disease, a minute protozoan parasite, and to prescribe the precautions necessary to avoid its occurrence.

Robert Koch (1843–1910) was a physician who early became interested in Pasteur's work. He invented special techniques for identifying and making pure cultures of bacteria. Because of its great economic importance Koch and Pasteur were led to work on a disease of sheep called **anthrax.** Koch was first to discover the causal organism, *Bacillus anthracis*, and to make a pure culture of it. Of more importance was his discovery that sheep could be made **immune** to the disease by injecting into them an old culture of the bacillus which had lost some of its virulence. This discovery led to the development of the **science of immunology,** to be referred to in a later section. These discoveries were made quite independently by Pasteur. Koch is also known as the discoverer of *Mycobacterium tuberculosus*, the cause of tuberculosis, a disease which unfortunately has not yielded to immunological methods.

Perhaps the best known work of Pasteur, certainly the most dramatic, is that on **rabies** or **hydrophobia**, the disease transmitted to man by the bite of a mad dog. By a method similar to that used in the case of anthrax, Pasteur was able to prevent the onset of the fatal symptoms of the disease by injections of gradually increasing strength from a culture of the filterable virus[1] which causes the disease.

The bodies of most animals, and the human body is no exception, contain numerous microorganisms. Some of these, especially those of the intestine, seem to be desirable or even necessary. Others may, on occasion, cause disease but are usually harmless. Still others, when present in sufficient numbers, nearly always cause disease. Bacteria which actually cause disease do so in one of three ways: by breaking down or **splitting protein** molecules and producing substances injurious to the body; by secreting **poisons** or **exotoxins**; and by forming within their protoplasm certain poisons or **endotoxins** which pass into the body of the host when the microorganisms die. In giving rise to a disease the bacteria may remain restricted to a certain part of the body as they do to the throat in diphtheria, or they may get into the blood stream and become generally distributed in the body as in the case of typhoid fever. In certain cases there may be a focus of infection in which bacteria persist and from which they may from time to time become distributed over the body. Frequent foci of infection are decayed teeth, diseased tonsils, and infected sinuses. Most diseases are specific and are caused by a particular species of organism; others like pus in a wound may be caused by any one or more of a group of organisms.

The proof that a specific microorganism is the primary cause of a disease is often difficult since other relatively harmless bacteria may be and often are present. From his work in discovering the tuberculosis bacillus and proving that it is the cause of this disease, Koch was led to put the requirements for the proof in the form of four postulates, called **Kochs' postulates:**

1. The microorganism must be present in all cases of the disease.
2. It must be isolated from the infected animal or man and grown in pure culture.
3. The original disease with its symptoms must be reproduced when the microorganism is injected into a susceptible host.
4. In the case of the induced disease, the microorganisms must be found as in the original case.

It has not always been possible to carry out this program in the investigation of diseases, but it represents the goal toward which investigators strive.

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[1] See later in this chapter under "filterable viruses."

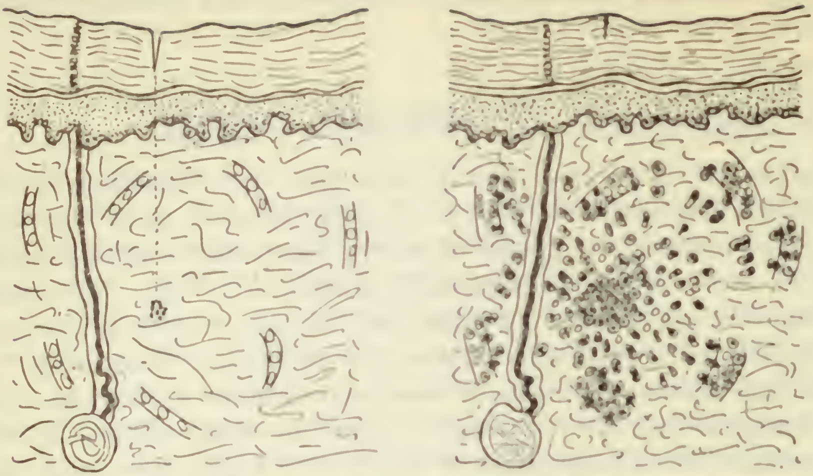
B. TRANSMISSION OF INFECTIOUS DISEASES

Each species of parasite usually has its own way of entering the body of its host. The particular part of the body where it gains entrance to the tissues is called the **portal of entry**. The evidence available shows that the intact skin is an impassable barrier to bacteria. Infection by bacteria through the skin is possible only when a cut, abrasion, or other interruption of its continuity exposes the underlying tissues (Fig. 9:10). A common portal of entry is the mucous membrane of the nose, throat, and windpipe and the respiratory epithelium of the lungs. This offers an entrance to the organisms of diphtheria, scarlet fever, meningitis, tuberculosis (Fig. 9:11), and probably also measles, smallpox, and infantile paralysis. The wall of the digestive tract offers another favorite portal. Here enter the germs of typhoid fever, dysentery, and cholera. The microorganisms causing hydrophobia, tetanus (lockjaw), and gas gangrene usually enter the tissues through a wound or scratch. Of all these portals of entry, that involving the respiratory tract is the most difficult to guard.

It is also important to know how pathogenic organisms leave the body. Many leave by the door at which they entered. Thus those which enter by the skin often leave by the same path when boils and sores open. Those which enter by the nose and throat leave in the mucus and other secretions coughed up or sneezed out. Those which enter by the intestinal tract leave in the feces.

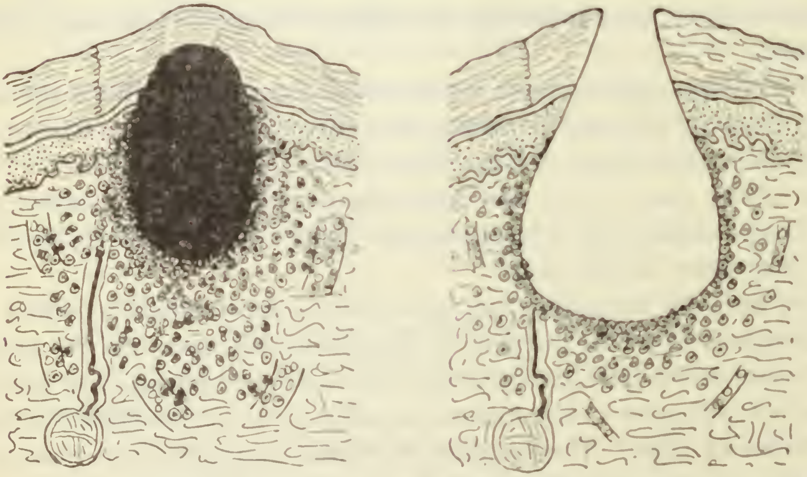
Most parasitic organisms can grow only in those tissues to which they are adapted. Thus the bacillus of diphtheria will grow on the mucous membrane of the back of the throat but not in the blood. The spirillum of cholera will grow in the mucous membrane of the intestine but not in the throat or blood. The bacillus of tetanus can grow in a wound but not on the intestinal mucous membrane or in the blood.

Fortunately in most cases the bacteria which cause human diseases are unable to grow and multiply outside the human body except under special conditions, conditions which are usually found only in the special methods of culture used in bacteriological laboratories. Thus the tetanus bacillus which causes lockjaw will grow only in the absence of oxygen, the influenza bacillus requires the presence of hemoglobin. However, some pathogenic bacteria are known to develop under exceptional cir-



1. A section of the normal skin just after it has been pierced by a dirty pin, carrying staphylococci through the epidermis into the dermis beneath.

2. The early stages of inflammation; migration of leucocytes from the swollen capillaries toward the infected area. The skin in this region is becoming red, swollen and painful.



3. The accumulation of leucocytes has continued and now there is a mass of purulent exudate about the germs. The boil has "come to a head" and the yellowish, semiliquid pus (black in the drawing) can be seen through the thin layer of epidermis which covers it.

4. The boil has finally ruptured and the pus has escaped, carrying with it the staphylococci. The migration of leucocytes has ceased and the capillaries are returning to their normal size. New tissue will fill in the cavity.

Fig. 9:10 The history of a boil. Adapted from C. P. Emerson, *Essentials of Medicine*, courtesy of J. B. Lippincott Company.

cumstances in milk, and the typhoid bacillus and the cholera spirillum may multiply under certain conditions in water.

Bacteria may be **transferred** in a variety of ways from one host to another causing the spread of the disease. Objects such as books, money, postage stamps, and letters which are passed from person to person may carry bacteria, but it is now generally recognized that their role has been much overemphasized. Dishes and bathroom appliances constitute a much greater risk. Hot water alone is not effective in killing bacteria. Soap is also necessary. Laundries have been shown to be a possible source of infection, especially when soiled clothes are collected and clean clothes delivered from the same wagon. At one time air was thought to play an important role in the spread of disease. Modern experimental work has tended to negative this. "Eminent students of public health have stated that there is no basis for the belief that those living about a hospital are more liable to have communicable disease."[1]

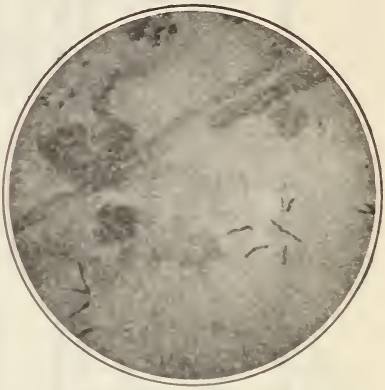


Fig. 9:11 The tubercle bacillus, the cause of tuberculosis. From Buchanan and Buchanan, *Bacteriology*, The Macmillan Company.

Contact between diseased and healthy persons is the most direct and usual method of spreading disease. The word "contact" is here used to include any direct transfer of infective material such as may occur when a recently used handkerchief is passed from one person to another, or a person coughs so as to scatter material onto another person. Many diseases are transmitted by **insects** — some diseases, e.g., yellow fever, only by insects. Many different kinds of bacteria are carried about by flies. Other diseases are transferred directly from higher animals to man, e.g., hydrophobia or rabies. Various articles of food, such as water, milk, fresh vegetables, and so on, may carry disease-producing bacteria and be a source of infection.

Certain people may carry the germs of a disease without showing any of the symptoms of the disease. This may happen before they "come down" with the disease or after they have recovered. There are, however, certain people who may be immune to a disease, but may nevertheless harbor the germs of the disease; these are the most dangerous kind and are called **carriers**.

[1] Tanner, F. W., *Bacteriology*, John Wiley and Sons, Inc., New York, 1937, p. 378.

TABLE 9:1 SOME COMMON COMMUNICABLE DISEASES[1]

DISEASE	GERM	SOURCE OF INFECTION	INCUBATION PERIOD	IMMUNITY
Chicken pox	A specific filterable virus	Sores on the skin of an infected person	2–5 weeks	Permanent immunity rare
Cholera	*Vibrio comma*	Discharges from digestive tract and carriers	1–5 days	Acquired immunity uncertain
Conjunctivitis (Pink eye)	*Gonococcus* or pyogenic bacteria	Discharges from conjunctiva or genital mucous membranes	Irregular 36–48 hours	No acquired immunity
Diphtheria	*Corynebacterium diphtheriae*	Discharges from the throat of an infected person and carriers	2–5 days	Acquired immunity after disease, also artificial active and passive immunity
German measles	Unknown — probably filterable virus	Secretion of mouth of infected persons	14–21 days	Acquired immunity permanent
Gonorrhea	*Neisseria gonorrhoeae*	Discharges from infected region	1–8 days	None known
Influenza	A filterable virus	Discharges from mouth and nose of infected person	24–72 hours	None known
Measles	A filterable virus	Secretions from mouth or nose of infected person	12–14 days	Acquired immunity permanent
Epidemic meningitis	*Neisseria intracellularis*	Discharges from nose and mouth of infected person	2–10 days	Acquired immunity after disease, passive immunity with antisera
Mumps	A filterable virus	Secretions of mouth of infected person	12–26 days	Acquired immunity after disease
Paratyphoid fever	*Salmonella paratyphi*; *Salmonella schottmulleri*	Discharges from the bowels and bladder	4–10 days	Acquired immunity good; also active by vaccination

[1] Modified from *Bacteriology* by F. W. Tanner, from a Report of a Committee of the American Public Health Assoc., Public Health Reports, Aug. 9, 1935.

TABLE 9:1. SOME COMMON COMMUNICABLE DISEASES (*Continued*)

DISEASE	GERM	SOURCE OF INFECTION	INCUBATION PERIOD	IMMUNITY
Plague	*Pastuerella pestis*	Blood of infected rodents; sputum of infected human cases	3–7 days usually	Acquired immunity after disease or vaccination
Pneumonia	Various pathogenic bacteria	Discharges from mouth and nose	1–3 days	Immunity relatively slight
Poliomyelitis (Infantile paralysis)	A filterable virus	Discharges from mouth and nose	7–14 days	Permanent immunity after disease
Rabies (Hydrophobia)	A filterable virus	Saliva of infected animals, chiefly dogs	2–6 weeks, up to 6 months	Prophylactic antirabic treatment
Scarlet fever	A hemolytic streptococcus	Discharges from mouth and nose or from abscesses	2–7 days	Acquired immunity after disease
Septic sore throat	A hemolytic streptococcus	Human cases; infected milk	1–3 days	Probably no immunity
Smallpox	A filterable virus	Sores on infected person	8–16 days	Permanent acquired immunity after disease; also after vaccination
Syphilis	*Treponema pallidum*	Discharges from sores	About 3 weeks	None
Tetanus (Lockjaw)	*Clostridium tetani*	Discharges from men and animals; infected soil	4 days to 3 weeks	Passive immunity after antitoxin; active after vaccination
Tuberculosis (pulmonary)	*Mycobacterium tuberculosis*	Mainly from sputum	Variable	Generally none
Typhoid fever	*Eberthella typhosa*	Bowel discharges of patients; carriers	3–38 days	Permanent acquired immunity after disease; active after vaccination
Whooping cough (Pertussis)	*Hemophilus pertussis*	Laryngeal and bronchial discharges of infected person	10–16 days	Prolonged immunity after disease
Yellow fever	A filterable virus	Bite of infected mosquito	3–6 days	Permanent after disease

C. RESISTANCE AND IMMUNITY

The introduction of a foreign protein, i.e., a protein not normally present in the tissues, into the tissues of an animal or plant may produce harmful results. In most cases, however, the harm is prevented by the production by the animal or plant of substances called **antibodies.** The antibodies nullify the effect of the foreign protein by combining with it to form some harmless substance, or causing its disintegration or precipitation. Any substance which when introduced into the tissues of an animal or plant stimulates the formation of antibodies is called an **antigen.** Thus if a solution of white of egg (albumin) is injected under the skin, a substance is developed by the body which precipitates the white of egg. Antigens and antibodies are specifically related, i.e., a given antigen stimulates the formation of a particular antibody, and a given antibody acts to counteract a particular antigen. The **toxins,** already mentioned as formed by bacteria and in large measure the cause of these injurious effects, act as antigens.

The body responds to bacterial invasion in two ways. (1) Certain of the white blood corpuscles and certain cells lining the body cavity have the power to surround, absorb, and digest bacteria and for this reason are called **phagocytes.** (2) In response to the presence of the extracellular and endocellular products of the bacteria, the body produces **antibodies,** which combat the activities of the bacteria. One kind of antibodies, called **antitoxins,** are produced in response to toxins. Another kind cause bacteria to gather in clumps and are called **agglutinins;** still another kind, called **opsonins,** render bacteria less resistant to the attacks of the phagocytes; a fourth kind immobilize bacteria and are called **precipitins** and a fifth kind, the **lysins,** dissolve bacteria.

It is common knowledge that when a number of people are exposed to infection, some show much more resistance than others. Such people are said to be **immune** and the resistance which their bodies offer to infection is called **immunity.** Immunity may be either natural or acquired. **Natural immunity** is something a person is born with. For example it is known that individuals of the white races are in general more resistant to tuberculosis than the negro; while on the other hand, the negro is more resistant to malaria than the white man. In any epidemic a number of individuals always escape. **Acquired immunity** is something acquired during one's lifetime. There are several ways in which immunity may be acquired, one of which is a previous attack of the disease Another way is by having the disease in a very mild form. This is the principle of vaccination for smallpox. The person who is vaccinated and in whom the vaccination has "taken" gets a mild attack of smallpox which appears only as a small pustule or pimple at the place of inoculation. This gives him an acquired immunity which may last for a number of years. If the vaccination does not "take," i.e., if the pustule does not appear, the person possesses a natural immunity to smallpox.

Immunity which is acquired by a previous attack of the disease is due to the fact that the body continues to produce antibodies after recovery from the disease. This kind of acquired immunity is called **active immunity.** An animal may be made immune by injecting into it the serum or plasma of an animal that has been made actively immune. The immunity so acquired, which is often very effective but of short duration, is called **passive immunity.**

The methods by which acquired immunity can be produced have become of great importance in the prevention and cure of disease. These may be briefly listed as follows:

1. Through recovery from the disease either contracted naturally or artificially produced. This immunity may be slight as after pneumonia, or more marked as after diphtheria and typhoid fever, or prolonged as after scarlet fever.

2. By inoculation with the weakened strain of the microorganism. An example of this is the vaccination for smallpox with a weakened form of the microorganism grown in the cow.

3. By the injection of the microorganism into tissues where they will not develop. An example of this is the injection of diphtheria bacilli, typhoid bacilli, or cholera spirilla just under the skin which was formerly the practice but has now been replaced by other methods of immunization. Although the bacteria are destroyed by the subcutaneous tissue, their products cause the production of substances which produce immunity.

4. By the injection of bacterial products or their dead bodies. An example is vaccination for typhoid fever by the injection of dead bacteria. Here again the bacterial products cause the production in the animal of immunizing substances.

The above four methods produce an active immunity. The following method produces a passive immunity:

5. By the injection of the blood serum of animals which have survived the disease or have been inoculated with bacterial products to induce the formation of antibodies. An example of this is the use of diphtheria and tetanus antitoxins.

Acquired immunity can be obtained to the following diseases: diphtheria, tetanus (lockjaw), rabies (hydrophobia), epidemic meningitis, typhoid fever, scarlet fever, smallpox, plague, cholera, measles, and probably whooping cough and chicken pox.

All factors, such as proper diet, exercise, fresh air, and so on, which contribute to maintaining the body in a healthy condition, also increase its resistance to bacteria, and in many cases attention to these factors is the only known preventive.

D. THE PREPARATION OF AN ANTITOXIN

A brief description of the preparation of **diphtheria antitoxin** will help in understanding the preceding discussion.

It is necessary first to obtain diphtheria toxin of known strength. To obtain this a virulent strain of the diphtheria bacillus, *Bacillus diphtheriae*, is grown in pure culture in broth (Fig. 9:12). After growth has continued for from five to nine days the maximum amount of toxin is produced. The broth is then filtered through a porcelain filter which allows the toxin to pass but keeps back the bacteria. Thus a sterile solution containing the toxin is obtained. By adding ammonium sulphate to this solution the toxin can be precipitated out. The precipitate is then dried in a vacuum and a powder obtained. This dried toxin does not deteriorate when kept. One gram of the powder may contain as much as 40,000 fatal doses. The strength of the toxin is determined by injecting it in solution into guinea pigs. The standard unit for diphtheria toxin is the amount which, on the average, when injected into a guinea pig weighing 250 grams will kill it at the end of four days.

The antitoxin which is used in the prevention and cure of diphtheria in human beings is obtained from the blood of horses kept especially for this purpose. Only young, vigorous, and absolutely healthy horses are used. Each horse is injected with gradually increasing doses of toxin until the maximum for each horse is reached. This maximum is determined by watching carefully the temperature and general condition of the horse. A small amount of blood is then taken from the horse and allowed to form a clot and the liquid portion or serum which contains the antitoxin is withdrawn under sterile conditions. The serum is then tested for its antitoxin content. Measured volumes of the horse serum are injected into guinea pigs simultaneously with unit doses of toxin and the amount of serum required just to neutralize one unit of toxin determined. If this test shows the antitoxin content of the blood to be satisfactory the horse is bled on a larger scale and larger quantities of serum obtained. A small quantity of preservative is added to the serum and it is ready to be put up in small sterile glass containers for distribution to physicians. The immunity conferred by the injection of the antitoxin is a passive immunity. It is now used chiefly in the treatment of the disease. When the antitoxin treatment is begun with sufficient amounts of the antitoxin on the first day of illness recovery from the disease is practically certain. For **active immunization** against diphtheria a mixture of toxin and antitoxin in a proportion to leave an excess of free toxin, was used, the pure toxin being too dangerous for use. This method was replaced by one in which diphtheria toxoid was used. The **toxoid** is obtained from the toxin by

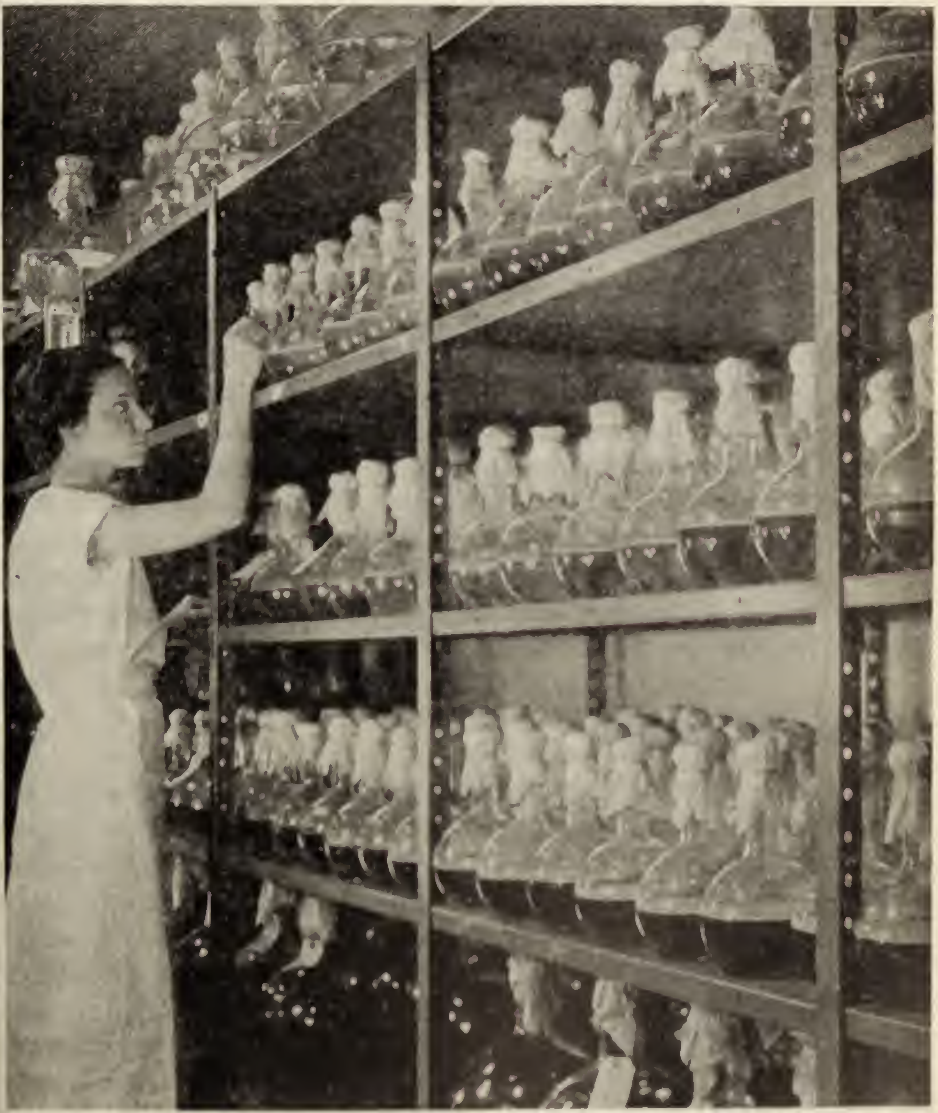


Fig. 9:12 Incubation of mass cultures in bouillon for the preparation of toxins. Photograph by the Park Davis Company.

treating it with heat and chemicals. It is nonpoisonous but is nevertheless capable of stimulating the formation of antitoxin. More recently a form of toxoid called **anatoxin** made by adding a small quantity of formaldehyde (0.4 per cent) to diphtheria toxin has been introduced. This has the advantage of not introducing horse serum, to which some people are sensitive (allergic).

Diphtheria is mainly or almost entirely a disease of childhood. The antitoxin treatment has been extraordinarily effective in reducing the mortality from this disease. Literally millions of children are saved each year by its application. The method of preparation of tetanus antitoxin is similar to that of diphtheria antitoxin.

10. ALLERGY

Some people break out with a violent rash over the body when they eat fresh strawberries, others get hay fever when the ragweed blooms in the autumn, and still others cannot sleep on a feather pillow. These are cases of **allergy** and the people are said to be allergic to strawberries, ragweed pollen, or feathers, as the case may be. They are really particularly sensitive, **hypersensitive,** to certain substances in these materials. In some instances drugs are the cause of allergic reactions. Thus skin rashes may follow the taking of quinine, or the application of iodine or mercuric chloride to the skin. Although not a strictly bacteriological phenomenon, allergy is sometimes of importance in the treatment of disease or in immunological procedures. Thus if a child is sensitive to horse serum great care may have to be exercised in administering diphtheria antitoxin.

11. FILTERABLE VIRUSES

Until quite recently a number of otherwise well-known diseases resisted all attempts to discover visible causal organisms. About thirty years ago a remarkable fact was discovered regarding one of these, a disease of the leaves of the tobacco plant, called, from the irregular way in which the young leaves are attacked, the **mosaic disease.** Diseased leaves were emulsified or finely ground up in water and the watery emulsion filtered through a very fine sterile filter known to stop the passage of bacteria. When some of the filtrate which was proved to contain no visible organisms was placed on healthy young leaves they soon showed the typical symptoms of the mosaic disease and a filtered emulsion made from their tissues was similarly effective in causing the disease in other tobacco plants. The results suggest that the cause of the disease whether it be a living organism or a nonliving molecular complex is of submicroscopic size. The general term, **filterable viruses,** has been applied to such agents. Some common diseases which are believed to be caused by filterable viruses are listed below.

Plants

Mosaic diseases of
  Tobacco
  Tomato

Animals

Hog cholera
Foot-and-mouth disease
Distemper of dogs

Man

Smallpox
Chicken pox
Infantile paralysis
Hydrophobia
Mumps
Measles
German measles
Common colds
Yellow fever

The filterable viruses possess certain characters in common which may be briefly stated as follows:

1. They increase or multiply only in the presence of living cells.

2. Their activity is specific, e.g., the tobacco mosaic virus attacks the leaves of the tobacco plant only.

3. They cause characteristic changes in the infected cells. This is especially true in the case of hydrophobia where the brain cells come to contain certain well-defined and positively identifiable bodies.

4. A high degree of immunity is conferred by an attack of most filterable virus diseases. This is well known in the case of smallpox. But the common cold seems to be an exception.

5. Most filterable virus diseases are highly infectious, i.e., are easily passed from host to host.

Recently a protein has been crystallized from an emulsion of diseased tobacco leaves which shows all the properties of the filterable virus and when applied to healthy leaves causes the mosaic disease. The question whether a filterable virus is a living organism is one which has yet to be answered for each particular case.

Possibly to be associated with the filterable viruses are **bacteriophages,** agents which are able to cause the destruction of bacteria. The discoverer of bacteriophage believes it to be an organism capable of passing through filters. Since their original discovery bacteriophages have been found to be widely distributed, almost as widely distributed as bacteria. Bacteriophages obtained from an individual who has just recovered from a germ disease are most active against the germ of the particular disease but may be active against other organisms. As a destroyer of bacteria, bacteriophage would seem to have practical application in the cure of bacterial diseases. So far this has not proved to be the case. Experimental studies have not shown that it has any effect on the course of such diseases. Recent work tends to show that bacteriophage is not a living organism but more probably a product of the metabolism of the bacteria, which, accumulating, causes their disintegration.

12. DRUGS AND BACTERIA

Most drugs merely work toward alleviating the symptoms of a disease rather than toward combating its primary cause, which in an infection is the bacteria or other parasitic organisms. However, there are a few substances which seem to be specific for certain diseases. One of the first of these to become known was **quinine**. This drug apparently acts directly to check the growth and increase of the malarial parasite (a protozoan and not a bacterium) in the blood. **Salversan** and **neosalversan** belong to a class of drugs containing arsenic and are used effectively against *Treponema pallidum*, the organism which causes syphilis. Recently the various "sulfa" drugs including **sulphanilamide, sulphapyridine,** and **sulphathiazole** have proved very effective against streptococcic infections, especially those occurring in wounds. They are organic compounds containing sulphur developed from a red dye named prontosil which was found to have bactericidal powers. Sulphanilamide is effective against infections due to certain types of streptococcus and meningococcus, sulphapyridine is very effective in certain types of pneumonia, and sulphathiazole is effective in staphylococcal infections. More recently a substance called penicillin, obtained from the mold *Penicillium natatum*,[1] has proved particularly valuable in the treatment of certain infectious diseases. Following this discovery other substances similarly effective against bacteria have been obtained from other molds or mold-like bacteria. The general term **antibiotic agents** is now applied to such substances.

Penicillin has proved to be effective against staphylococci, streptococci, pneumococci, gonococci, meningococci, and the organism causing gas gangrene. Through its use infections which formerly required weeks or months for treatment can be treated in a matter of hours or days. It has proved very effective in many infections which resist treatment with "sulfa" drugs. Penicillin acts to combat the bacteria, the real cause of the disease, rather than merely to alleviate distressing symptoms.

[1] See Chap. 17 for a brief description of the preparation of penicillin.

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Questions

1. Discuss the morphology of bacteria.
2. How would you proceed to study the bacteria present in a sample of water? Suggest how you would apply the method to a sample of milk.
3. Discuss the autophytic bacteria in the soil. What is chemosynthesis?
4. Outline the modern method of sewage disposal.
5. Describe three methods for the preservation of food. Explain the bacteriological principles involved.
6. Discuss the uses of bacteria in industry.
7. How do bacteria cause disease?
8. State Koch's postulates for the proof that a specific organism is the cause of a disease.
9. Name the important "portals of entry" for bacteria and diseases which enter at each portal.
10. Discuss the transfer of bacteria from one host to another host.
11. How does the body combat disease?
12. Classify the kinds of immunity and state how each kind is brought about.
13. Name ten diseases to which immunity can be acquired.
14. Describe a method of obtaining diphtheria antitoxin.
15. Discuss the filterable viruses from the point of view of (*a*) diseases which they cause, (*b*) their nature.

Suggestions for Further Reading

Buchanan, Eslette D., and Robert E. Buchanan, *Bacteriology*, The Macmillan Company, New York, 1930. An elementary text with emphasis on everyday problems.

Tanner, Fred Wilbur, *Bacteriology*, John Wiley and Sons, Inc., New York, 1937. A general text including agricultural applications.

Burdon, Kenneth L., *A Textbook of Bacteriology*, The Macmillan Company, New York, 1937. A readable text with emphasis on the medical aspects.

CHAPTER 10

Liverworts and Mosses (Phylum Bryophyta)

The thallophytes considered in the two previous chapters are mostly plants which live in water or decaying organic matter which contains water. For such a habitat a thallus is well adapted. Rigidity of structure would have no advantages; indeed, it would be a decided disadvantage to a floating plant. Since most of the cells are comparatively near their source of food supply, the conduction of water and food materials through the plant is not usually of sufficient importance to demand special conducting tissues.

The earliest plants were undoubtedly thallophytes living in the shallow water on the shores of lakes or seas. From them developed the land plants. However, life on land is a very different matter from life in water. Only very gradually did plants become adapted to life on land and the process took a very long time. We can reconstruct a number of the steps in this process by studying some of the primitive land plants which have not become completely adapted to a land life. The familiar mosses and the less familiar liverworts are such plants.

1. THE LIVERWORTS (CLASS HEPATICAE)

Liverworts are small inconspicuous plants which grow best in moist, shaded places, on the ground, on rocks, on trees, or even floating on the surface of the water of bogs. A convenient type to study is *Marchantia.*

A. THE LIFE CYCLE OF MARCHANTIA

(1) THE GAMETOPHYTE

Marchantia grows on the ground in moist places, near springs or waterfalls. Its plant body reminds one of the thallus of an alga. It is a flat branching structure, bearing on its under side many hairlike structures called **rhizoids** from their resemblance to roots. Growth occurs by the division of certain cells located in notches at the ends of the branches.

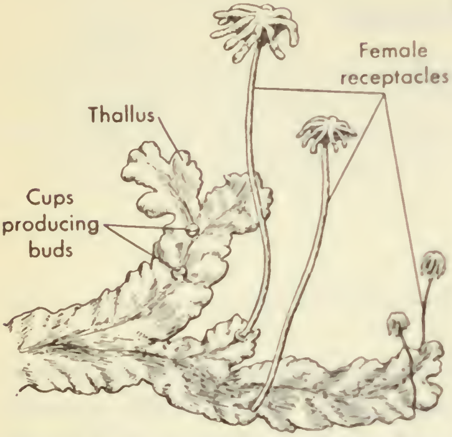

Fig. 10:1 A liverwort, *Marchantia*. Female gametophyte. Redrawn after Bergen and Davis, *Principles of Botany*, Ginn and Company.

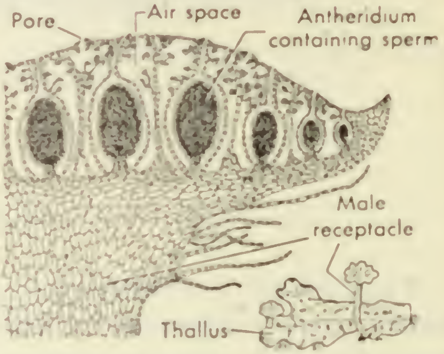

Fig. 10:2 *Marchantia*. Male gametophyte and section of receptacle showing antheridia. Redrawn after Pool, *Basic Course in Botany*, Ginn and Company.

Asexual reproduction of the gametophyte may occur by means of many-celled **buds** which are given off from the bottom of cuplike bodies on the upper side of the thallus (Fig. 10:1). These buds develop into new plants similar to their parents.

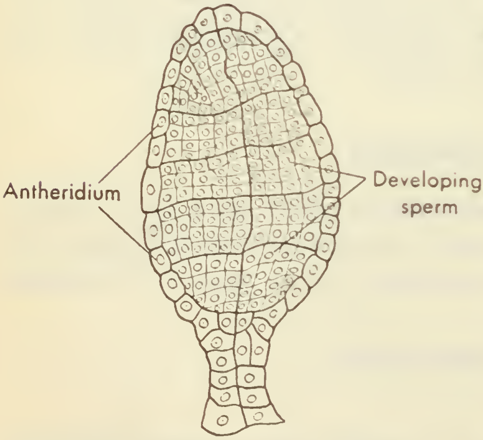

Fig. 10:3 *Marchantia*, an antheridium.

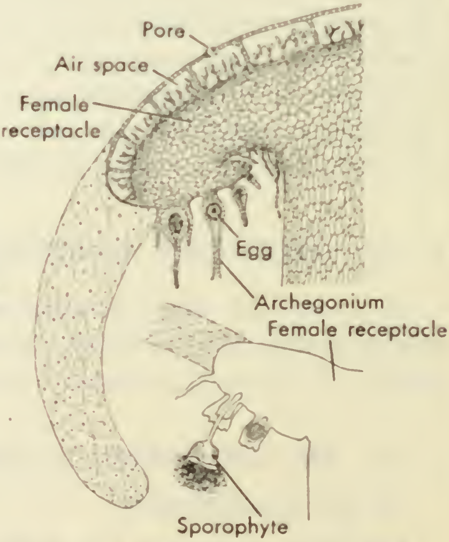

Fig. 10:4 *Marchantia*. Sections of female receptacles showing, above, archegonia, and below, sporophytes.

(2) SEXUAL REPRODUCTION

The marchantia plant also reproduces sexually by means of gametes and because it does so it is called a **gametophyte** (Gr. *gamete*, wife + *phyton*, plant). The sexual organs are multicellular and are developed on stalked umbrellalike organs called **receptacles.** Male and female organs are not found on the same plant. The **antheridia** or male reproductive organs are formed in pits on the top of the male receptacles (Fig. 10:2). Each one consists of a multicellular stalked sac in which numerous sperms are developed (Fig. 10:3). The female organs or **archegonia** grow out on the underside of the female receptacles (Fig. 10:4). They are flask-shaped and the body of the flask or **venter,** which contains the single egg, is attached to the receptacle, while the neck of the flask hangs downward. Water is necessary for fertilization in order that the sperm may reach the archegonium and swim up its neck to the egg.

(3) THE SPOROPHYTE

The fertilized egg or zygote remains in the archegonium and develops there into a new plant entirely dependent on its parent for its food and water which it absorbs through a special organ called the **foot** (Fig. 10:4). Because it forms spores this plant is called a **sporophyte**. The spores which it produces develop into gametophytes similar to the marchantia plant with which the description started.

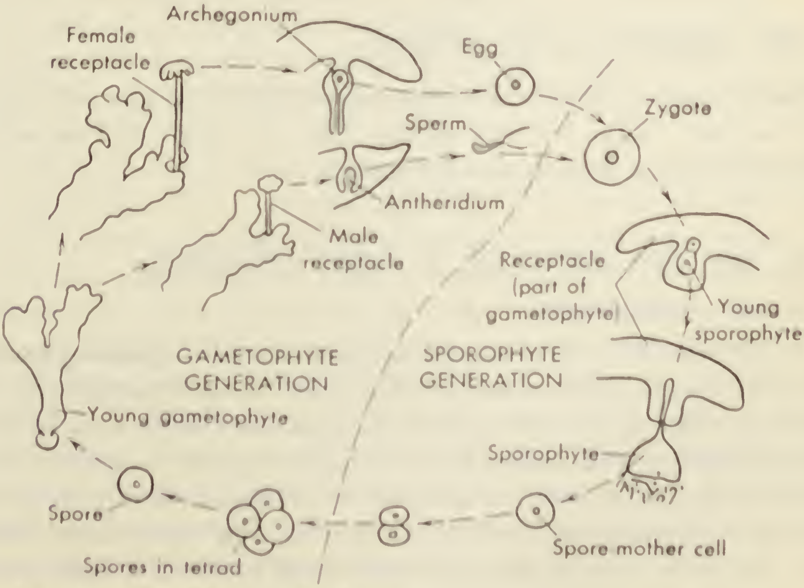

Fig. 10:5 The life cycle of a liverwort.

(4) SUMMARY OF THE LIFE CYCLE OF A LIVERWORT

The life cycle of a liverwort is summarized in the diagram (Fig. 10:5). A gametophyte generation alternates with a sporophyte generation. The spore develops into a gametophyte which may bear either male or female receptacles. The male receptacles bear antheridia in which numerous sperms develop. The female receptacles bear archegonia in each of which a single egg develops. The egg is fertilized in the archegonium. The zygote develops into a sporophyte which gives rise to spores which develop into sporophytes and continue the cycle.

B. OTHER LIVERWORTS

One of the simplest of liverworts is *Riccia.* This genus grows on moist ground or floats on water. The sex organs develop on the surface of the thallus. The sporophyte takes the simple form of a sphere of cells in the interior of which spores are formed. Probably the most highly developed liverwort sporophytes occur in Anthoceros. In this genus they take the form of tall stalks, the spore-forming cells extending through the axis. Certain of the cells of the sporophyte contain chlorophyll so that the plant is not entirely dependent on the gametophyte for its food. One group of liverworts, called **leafy liverworts,** are frequently mistaken for mosses because the thallus is differentiated into a branching stem with mosslike leaves. The sporophyte, however, is that of a typical liverwort.

2. THE MOSSES (CLASS MUSCI)

Mosses are more widely distributed than liverworts and some of them have become adapted to dry places. The life history of *Funaria*, a not uncommon genus, is typical of the group.

A. THE LIFE CYCLE OF A MOSS (FUNARIA)

(1) THE GAMETOPHYTE

The life cycle of a moss includes two generations: a **gametophyte** generation in which gametes are produced and a **sporophyte** generation which produces spores. The leafy moss plant as usually seen belongs to the gametophyte generation. Such a leafy moss plant consists of a stem which usually grows erect, bearing leaves arranged spirally on its upper part and at its lower end rootlike filamentous outgrowths called **rhizoids** (Gr. *rhiza*, root + *eidos*, like). The stem and leaves of a moss are comparatively simple structures. Only in the midribs of the leaves and in the axis of the stem are the cells differentiated to perform special functions. Here occur elongated cells adapted for the conduction of water.

(2) SEXUAL REPRODUCTION

The sexual organs of the moss are borne on the tips of the stems. In most species, the male and female organs develop on different stems, but in some they occur on the same stem.

The leaves near the tip of the stem of a mature male branch are spread apart so that the male sexual organs called **antheridia** appear as an orange-colored spot in the center, giving to the whole tip the appearance of a miniature flower (Fig. 10:6). The orange-colored spot in the center contains several antheridia together with a number of club-shaped bodies called **paraphyses** (Fig. 10:7). Each antheridium is borne on a short stalk and consists of an elongated sac composed of a single layer of irregular flattened cells surrounding a central mass of cells. From the central mass of cells are developed a large number of small curved sperms or **antherozoids.** When sufficient moisture is present and the antherozoids are ripe the antheridium bursts open at its upper end, discharging its contents.

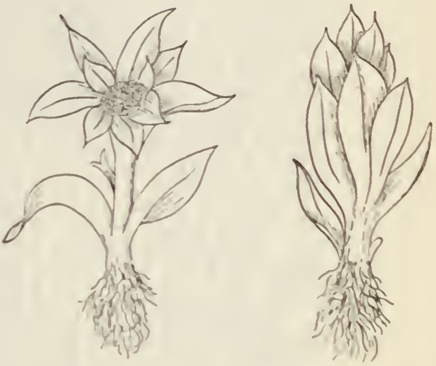

Fig. 10:6 A moss, *Funaria.* Male and female gametophytes. Redrawn from Mottier, *Textbook of Botany*, by permission of P. Blakiston's Son and Company.

The tips of the stems bearing the female sexual organs are covered by leaves (Fig. 10:6). The individual organs, called **archegonia** (Fig. 10:8), are flask-shaped structures. Each is borne on a stalk and consists of a **venter** and a **neck.** In the venter is a relatively large egg cell. In the axis of the neck are canal cells which, when the egg becomes ripe, break down into a mucilaginous mass filling a canal, the **neck canal.**

Fertilization can occur only when enough water is present for an antherozoid to swim from an antheridium to an archegonium. In the case of certain mosses it is not difficult to show that the antherozoids swim toward certain substances such as cane sugar which may be given off from the ripe archegonium. The antherozoids swim down the neck of the archegonium and one of them enters the egg, fertilizing it.

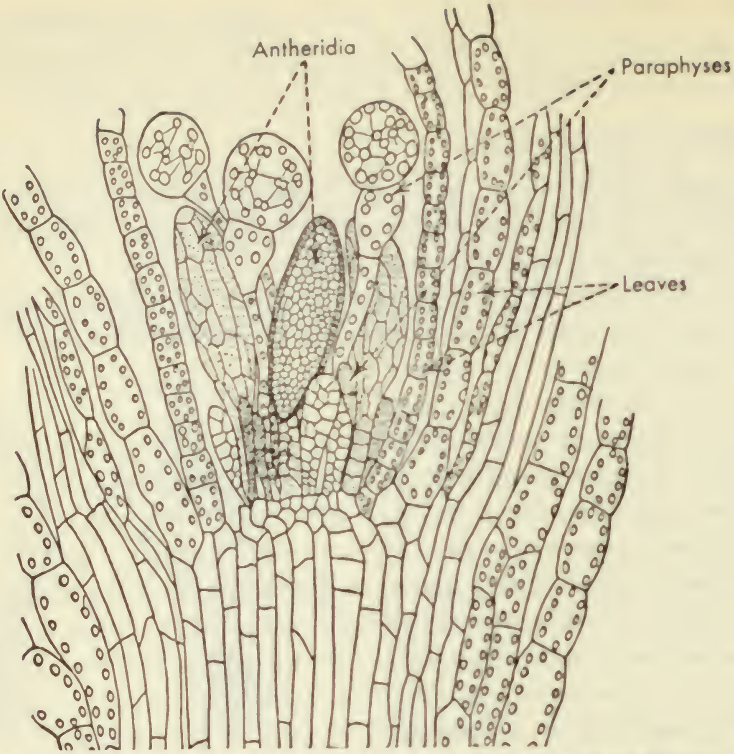

Fig. 10:7 *Funaria.* Male sexual organs of a moss. After Sachs, from Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

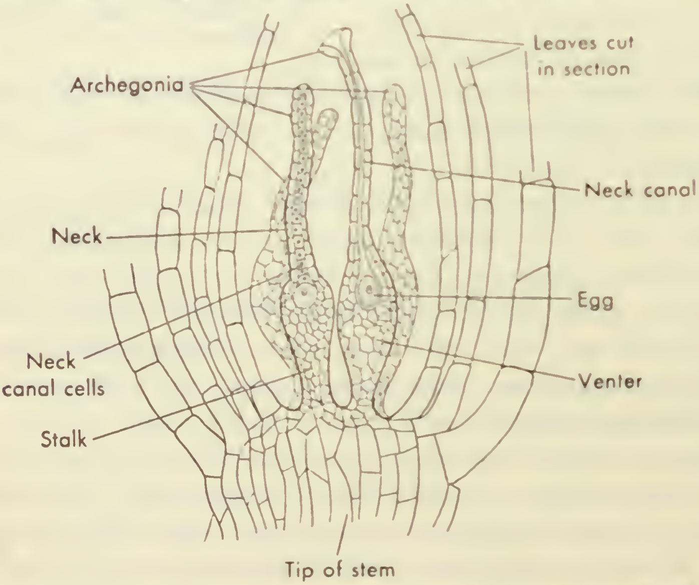

Fig. 10:8 *Funaria.* Female sexual organs of a moss. Redrawn from Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

(3) THE SPOROPHYTE

After fertilization has occurred the zygote begins immediately to grow into a **sporophyte** by cell division and cell growth, while still within the archegonium, developing eventually into an elongated **embryo** with an apical cell oriented toward the neck of the archegonium. The part of the embryo sporophyte in the lower portion of the archegonium differentiates into a **foot** which eventually penetrates into the tissues of the gametophyte and absorbs water and other food materials from it. The intermediate portion grows rapidly in length and forms a long slender **stalk**, or **seta**, the axis of which contains elongated conducting cells. The portion oriented toward the neck of the archegonium differentiates

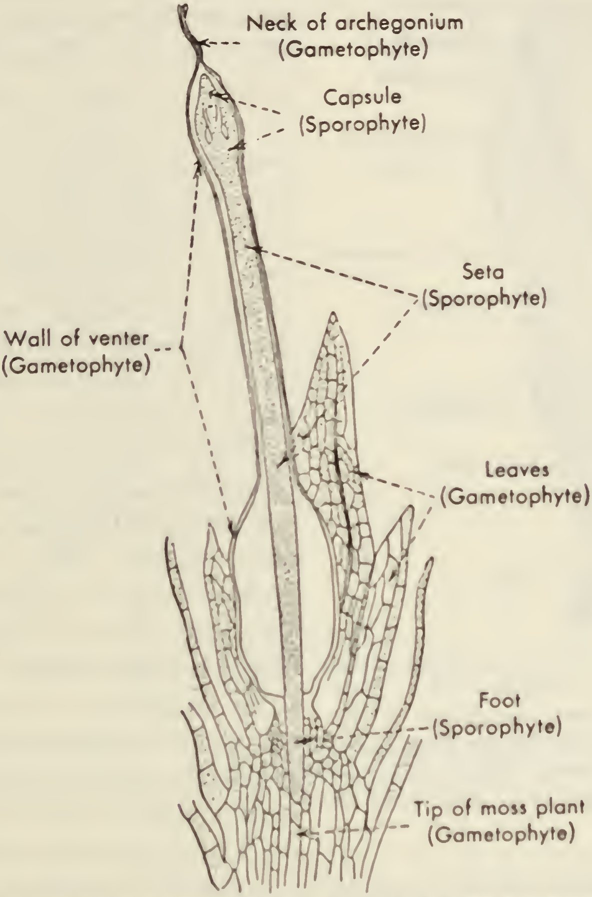
Neck of archegonium (Gametophyte)
Capsule (Sporophyte)
Seta (Sporophyte)
Wall of venter (Gametophyte)
Leaves (Gametophyte)
Foot (Sporophyte)
Tip of moss plant (Gametophyte)

Fig. 10:9 The tip of a female gametophyte branch of a moss and an advanced sporophyte as seen in longitudinal section, semidiagrammatic. The stippled structure is the sporophyte. After Sachs, from Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

into a **capsule** containing spores (Fig. 10:9). As the sporophyte grows in size the wall of the old archegonium, which grows at a corresponding rate, continues to enclose the young sporophyte until the stalk attains a considerable length when it breaks away around the base and is carried up as a caplike structure or **calyptra** covering the capsule.

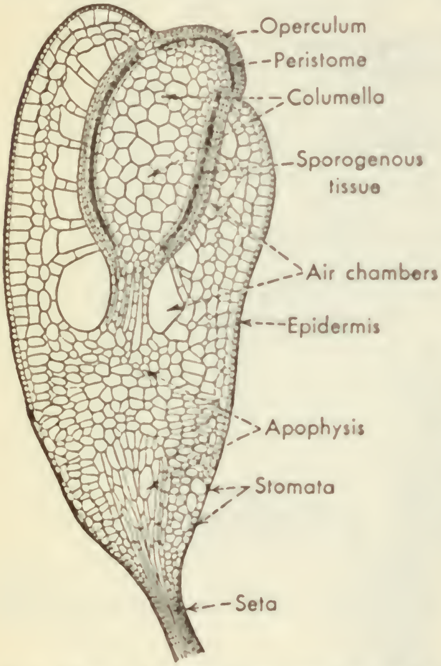

Fig. 10:10 Longitudinal section of the capsule of the sporophyte of a moss, *Funaria*. The spores are formed in the sporogenous or spore-forming tissue. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

It is in the capsule that the greatest differentiation of the sporophyte occurs (Fig. 10:10). The amount of spore-forming tissue in the capsule is relatively small, much space being taken up by other kinds of tissue. The central portion of an immature capsule consists of storage and conducting tissue, the upper portion of this tissue which is called the **columella** is surrounded by a cylindrical layer of **spore-forming tissue.** Outside this again are a number of layers of tissue containing **intercellular air spaces** and cells containing **chloroplasts.** The sporophyte is thus able to carry on a limited amount of photosynthesis. The spore-forming tissue develops first into **spore mother cells.** Each spore mother cell divides into four cells each of which becomes a **spore.** When the spores are formed the cells of the columella disintegrate leaving the spores free in the capsule. While water is essential for the sexual reproduction of the moss, the effective distribution of the asexually produced spores requires that they be dry and not stuck together in clumps as would be the case were they wet. The upper end of the capsule is differentiated to form a mechanism by which the spores can pass out of the capsule only in dry weather. The outer layer of cells at the upper end of the capsule forms a lid, called the **operculum,** which dries up and is cast off when the spores are ripe. Within the operculum are other layers of cells which form a **ring of teeth** pointing toward the central portion which becomes the opening of the capsule. These teeth are made up of rows of cells which react to the presence of moisture. When the humidity is high, i.e., the atmosphere is moist, the teeth bend in toward the interior of the capsule, closing the opening and adhering to the spores. When the humidity is low, i.e., the atmosphere is dry, the teeth bend outward, opening the capsule and carrying out with them any spores which have adhered.

(4) THE PROTONEMA

When the spore of a moss plant germinates, it gives rise to a structure called the **protonema** (Gr. *protos*, first + *nema*, a thread) which resembles a branched filamentous alga (Fig. 10:11). At intervals along the length of the protonema knoblike groups of cells called **buds** arise. From these buds are developed leafy moss plants. The gametophyte generation of the moss therefore includes in addition to the leafy moss plant, the protonema.

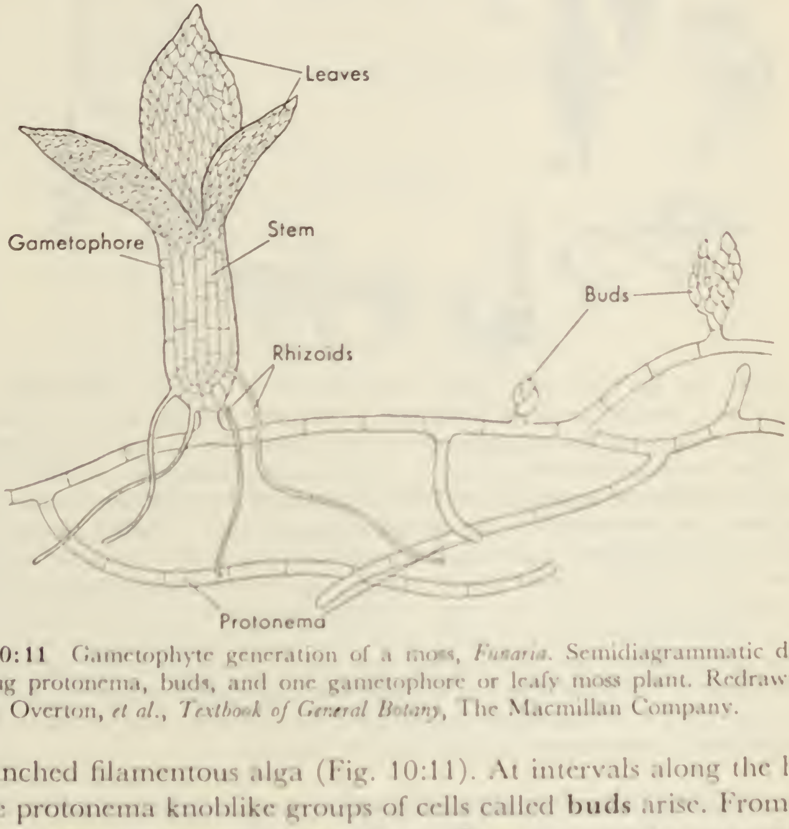

Fig. 10:11 Gametophyte generation of a moss, *Funaria*. Semidiagrammatic drawing showing protonema, buds, and one gametophore or leafy moss plant. Redrawn from Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

(5) SUMMARY OF THE LIFE CYCLE OF A MOSS

The life cycle of a moss consists of an alternation of generations — a sexually reproducing, gametophyte generation alternating with a spore-producing sporophyte generation (Fig. 10:12). The spore (12) germinates (13) into a protonema (14) which gives rise to buds which grow into leafy moss plants (1), which bear antheridia (2b) from which sperms (3b) are liberated and archegonia (2a) in which eggs (3a) are formed. The zygotes (4) develop in the archegonia into embryo sporophytes (5) which grow in length (6) and differentiate into foot, stalk, and capsule (7).

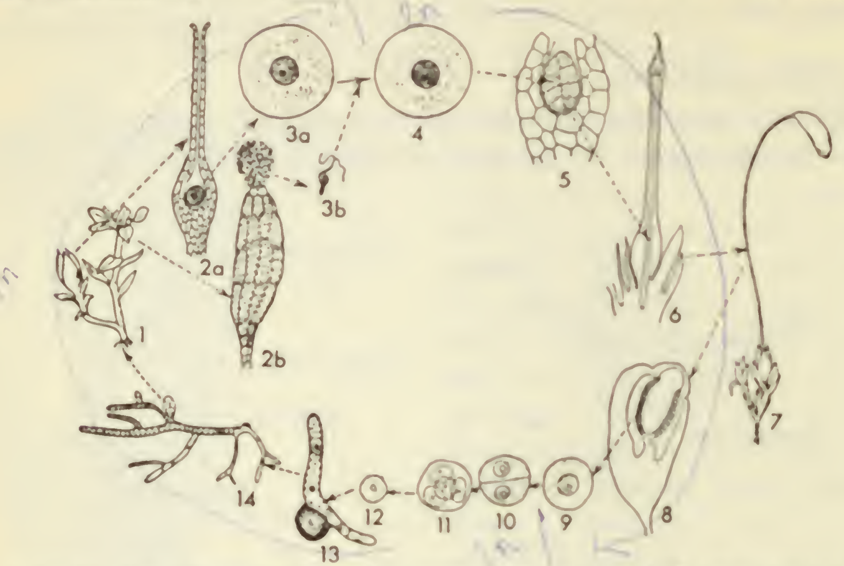

Fig. 10:12 The life cycle of a typical moss, *Funaria*. 1, the leafy gametophyte plant (gametophore), showing an antheridial and archegonial branch. 2a, an archegonium with a mature egg and 2b, an antheridium with sperm. 3a, an egg and 3b, a sperm. 4, the zygote resulting from their fusion. 5, a young embryo sporophyte within the venter of the archegonium. 6, sporophyte in advanced stage of development, attached to the gametophyte and surrounded by the enlarged archegonium. 7, mature sporophyte attached to the gametophyte. 8, section of the sporophyte capsule showing the location of the spore mother cells. 9, a spore mother cell. 10, two cells resulting from reduction division of the spore mother cell. 11, tetrad of spores resulting from the division of the two cells. 12, a single spore. 13, germinating spore showing protonemal thread and rhizoid. 14, older gametophyte plant showing the buds which develop into the leafy shoots of the gametophyte. The stages from 4 to 9 belong to the sporophyte generation, those from 12 to 14 and 1 to 3 to the gametophyte generation. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

In the capsule (8) are developed the spore mother cells (9) which divide first into two cells (10), then into four cells (11), each of which becomes a spore (12).

B. OTHER MOSSES

Nearly all mosses fall into one of two groups, the common mosses (order Bryales) and the peat mosses (order Sphagnales). The type chosen for description, *Funaria*, is one of the common mosses. The peat mosses, as their name implies, occur in swamps. There they often make up a considerable part of the vegetation. Their gametophytes have long stems and delicate leaves. Their sporophytes are somewhat simpler in structure than those of the common mosses.

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Questions

1. Why is the sporophyte of a moss considered to be a separate plant although it remains attached to the gametophyte?
2. What is achieved in the life cycle by the sporophyte of a liverwort or moss? What is achieved by the gametophyte?
3. Compare a liverwort and a moss in regard to (*a*) gametophyte stages, (*b*) sporophyte stages.
4. Which would you regard as the more highly evolved, a liverwort or a moss, and why?
5. What in the life cycle of the liverworts and mosses suggests that they were evolved from water plants?
6. How does the gametophyte of a liverwort differ from an alga?
7. Why do mosses never grow to a great height above the soil?

CHAPTER 11

The Ferns and Their Relatives (Phylum Pteridophyta)[1]

The ferns have advanced considerably beyond the liverworts and mosses in adaptation to life on land. This is particularly true of the sporophyte which has become a large independent plant.

1. THE FERNS (CLASS FILICINEAE)

A. THE LIFE CYCLE OF A FERN (POLYPODIUM)

In the fern the most conspicuous and familiar stage in the life cycle is the sporophyte. The discussion of the life cycle is therefore commenced at this stage rather than at the gametophyte stage as was done in the case of the liverworts and mosses, where the gametophyte stage was the most conspicuous and familiar.

(1) THE MATURE SPOROPHYTE

All that one sees above ground of an ordinary fern are the leaves, which in this case are often called **fronds**. The stem from which the fronds arise is underground, and in the common wild ferns runs horizontally (Fig. 11:1) several inches below the surface. Such an underground stem is called a **rhizome** (Gr. *rizoma*, a mass of roots). In some species and especially in the potted varieties the rhizome may be short and on the ground. In the tropics and some parts of the Southern Hemisphere (Tasmania) tree ferns occur with erect cylindrical stems which may reach a height of 40 feet.

The tip of the stem is the growing region and new leaves arise there. In temperate countries like the northern United States, the leaves of most ferns die down in the fall and new leaves grow up in the spring. The new leaves arise near the tip of the stem and at first are rolled up in a very characteristic way, reminding one of the curved end of a violin scroll. A frond consists of a relatively long stalk and a blade which is usually divided into numerous leaflets or **pinnae.** The underground stem bears in addition to the leaves numerous fine **roots.** A microscopic study of the stem and leaves shows that the cells are differentiated into tissues. These tissues resemble the tissues of the seed plants which will be studied in detail in a later chapter.

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[1] If the mosses have been studied in detail, Chap. 12, The Alternation of Generations and Its Significance, may be read before this chapter.

On the under side of the leaves occur brown spots, called **sori** (singular, sorus). Magnified, a sorus is seen to be a group of **sporangia** (Fig. 11:2). Each sporangium consists of a slender **stalk** and a **capsule.** The capsule is lens-shaped, the stalk being attached to the rim. The wall of the capsule is composed of a single layer of cells which are thin-walled except for a band of cells which form a portion of a ring, or **annulus** (L. *anulus*, a ring), around the rim (Fig. 11:3). The walls of the cells of the annulus are thick between the individual cells and toward the center of the capsule, while the outer cell walls are thin. The portion of the rim of the capsule not covered by the annulus contains two **lip cells. Spore mother cells,** usually sixteen in number, develop in the interior of the capsule. Each spore mother cell divides by two successive cell divisions into four spores, which for a time may remain to-

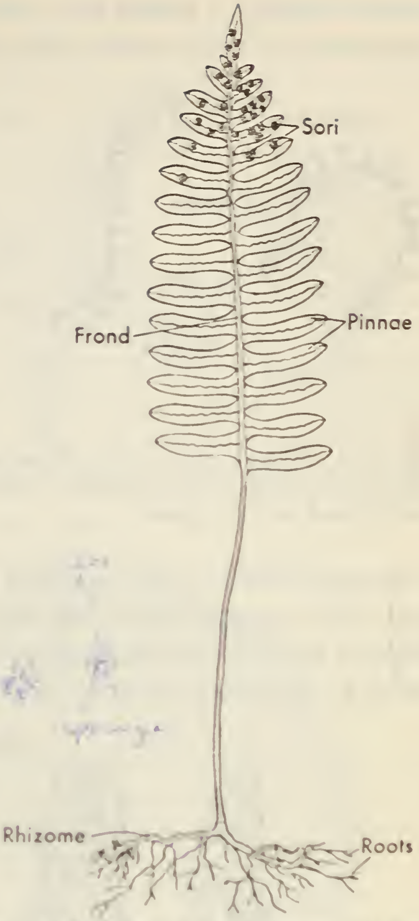

Fig. 11:1 A frond and rhizome of a fern, *Polypodium vulgare.*

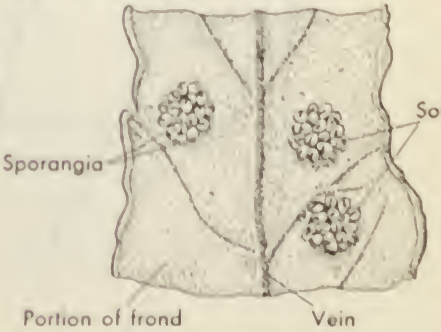

Fig. 11:2 Frond of a fern, *Polypodium,* bearing three sori each containing a number of sporangia. Redrawn from Holman and Robbins, *Textbook of General Botany,* by permission of John Wiley & Sons, Inc.

gether forming a **tetrad** (Gr. *tetras*, four) **of spores.** The ripe capsule bursts open in dry weather along a line separating the two lip cells. This is brought about by the annulus. In dry weather the cells of the annulus lose water through their thin outer walls. Since the inner and radial walls of the cells do not contract the decrease in volume causes the annulus to straighten out and curve over, opening the sporangium at the

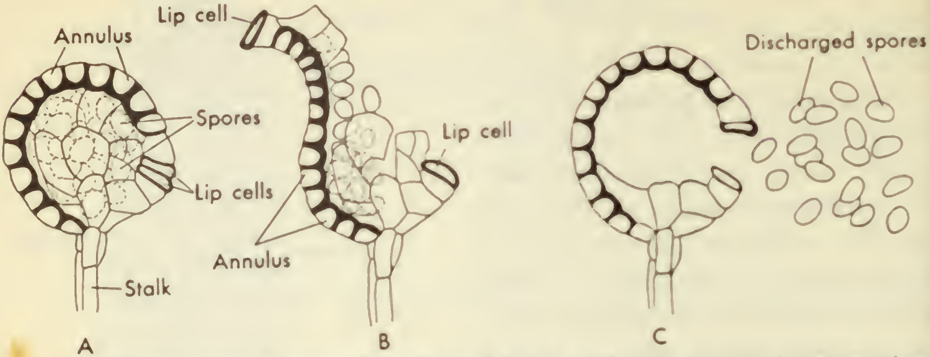

Fig. 11:3 Sporangium of a fern, *Polypodium*, showing method of opening the sporangium and ejecting spores. A, sporangium before opening; B, sporangium open; C, annulus springs back, ejecting spores.

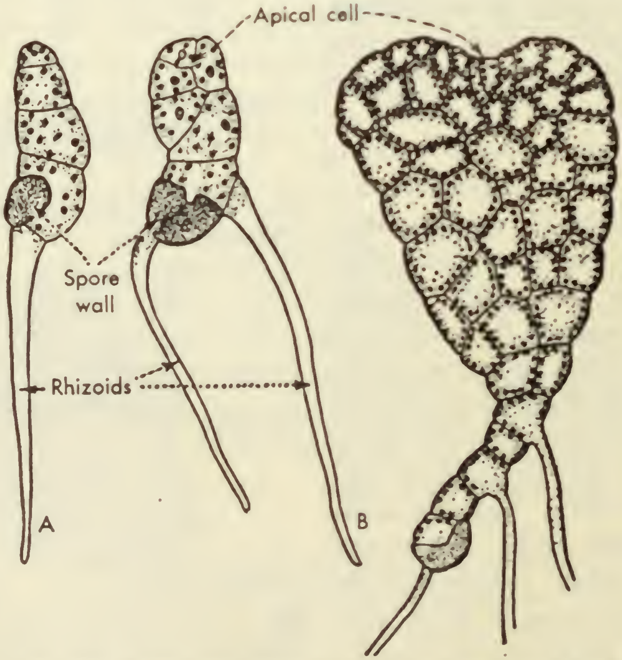

Fig. 11:4 Early stages in the development of the gametophyte of a fern, *Polypodium*. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

lip cells and tearing the side walls. Later the annulus springs back to its original position scattering any spores still in the ruptured sporangium (Fig. 11:3 B). The minute spores can float for a considerable time in the air and are dispersed by the wind. Because it gives rise to spores, the stage in the life of the fern which we have been considering is called a **sporophyte.** A leaf which bears sporangia is called a **sporophyll.**

(2) THE GAMETOPHYTE

When the spore of a fern germinates it becomes the gametophyte, so called because it is the generation which produces the gametes. In the ferns, this structure is also called a **prothallium** (Fig. 11:4). Prothallia grow on moist ground and are so small that they are seldom seen except by those especially in search of them. They are green in color and as they lie on the ground resemble minute leaves, with which, however,

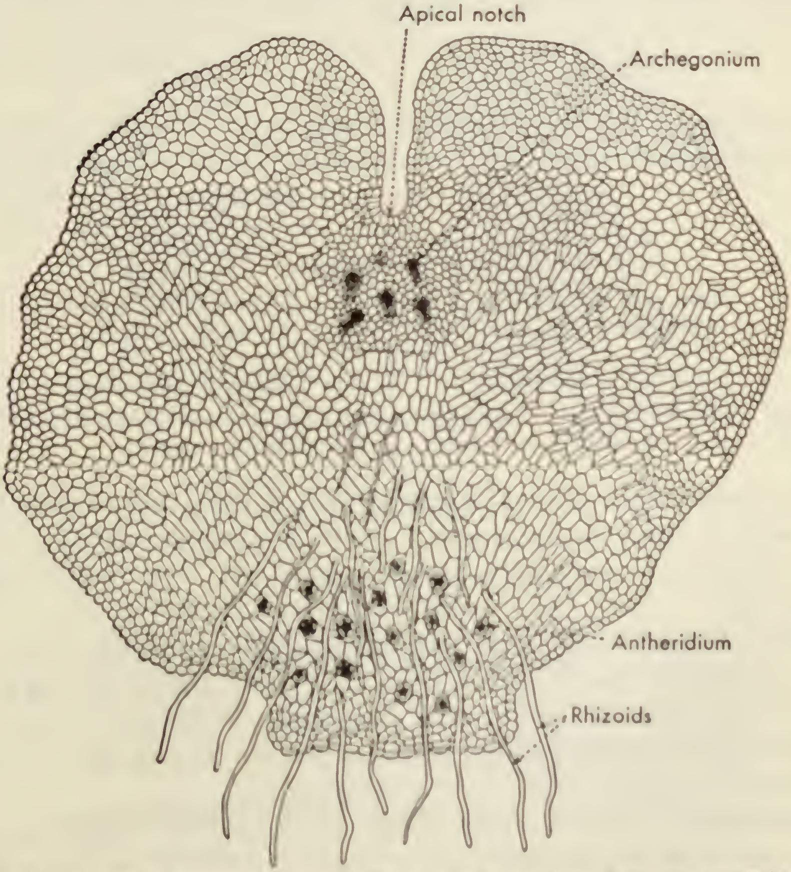

Fig. 11:5 Mature gametophyte, prothallium, of a fern as seen from the ventral surface. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

they have little in common. When mature, they are sometimes described as heart-shaped but are often more nearly circular with a notch at one end (Fig. 11:5). At the bottom of the notch is the region of most active cell division. This end of the prothallium is called **anterior.** At the other end, called **posterior,** and in the middle, numerous **rhizoids** arise from the under side. These are elongated hair-like cells which grow from the prothallium down into the ground. They serve to anchor the prothallium and to absorb water and dissolved substances from the ground.

(3) SEXUAL REPRODUCTION

The male sexual organs or **antheridia** occur on the under side of the prothallium among the rhizoids. The female sexual organs or **archegonia** are found on the under side at the anterior end near the notch.

The **antheridia** of a fern are small spherical bodies which project downward from the surface. A single layer of chlorophyll-bearing cells forms a jacket which encloses a mass of cells, usually thirty-two in number, each of which develops into a sperm or **antherozoid** (Fig. 11:6.) The antherozoids are small, spirally coiled cells with many flagella at one end.

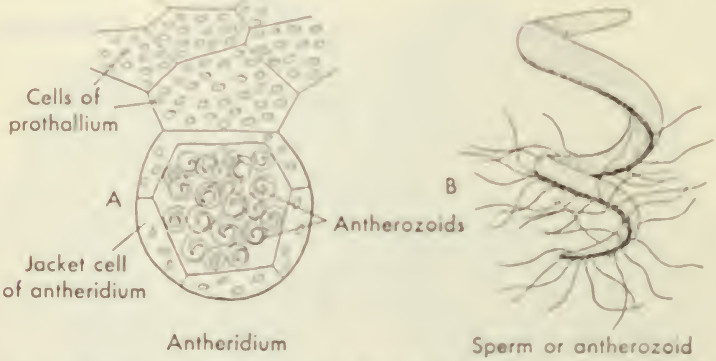

Fig. 11:6 A, an antheridium of a fern; B, a sperm or antherozoid. Redrawn from Smith, Overton, *et al., Textbook of General Botany,* The Macmillan Company.

The **archegonia** are partly imbedded in the prothallium, only the neck projecting from the surface (Fig. 11:7). Each contains an **egg** and, in the axis of the neck, a number of **canal cells.** As the egg becomes ripe the latter disintegrate, leaving the canal free for the passage of the antherozoids.

Fertilization, i.e., the union of the sperm with the egg, can occur only when there is sufficient water present for the sperm to swim to the neck of the archegonium. In the case of the ferns it has been shown experimentally that the sperms are attracted by malic acid and it is believed that this or some similar substance is formed by the disintegration of the canal cells. Fertilization of the egg occurs while it is still in the archegonium and the **zygote** undergoes its early development there. While still in the archegonium, the zygote begins to develop into a sporophyte, i.e., the familiar fern plant.

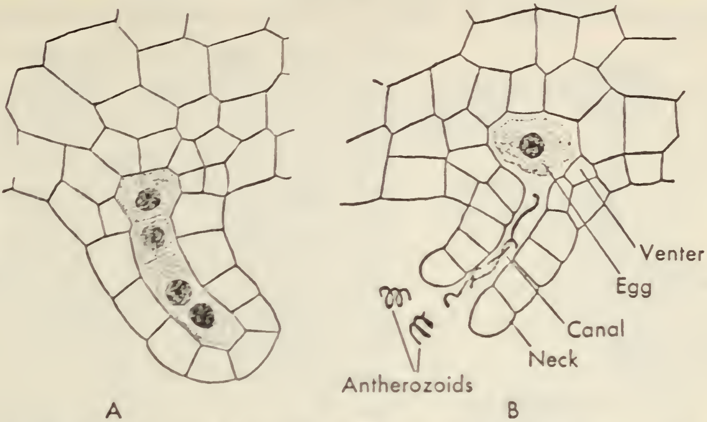

Fig. 11:7 The fern. A, nearly mature archegonium; B, archegonium at the time of entrance of antherozoids. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

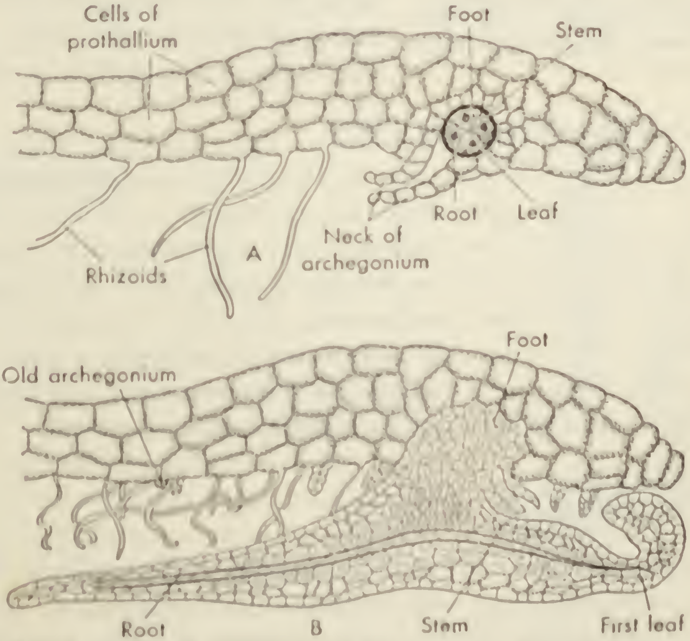

Fig. 11:8 Stages in the development of the sporophyte of a fern. A, four-celled stage; B, later stage. Redrawn from Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

(4) THE YOUNG SPOROPHYTE

The different parts of the sporophyte are early determined. The single cell resulting from the union of the egg and sperm divides first into two and then into four cells. Each of these four cells gives rise to a different part of the sporophyte (Fig. 11:8). One gives rise to the **stem,** another to the first **leaf,** a third to the **root,** and the fourth to a structure called the **foot** which grows into and absorbs nourishment from the prothallium. The young sporophyte grows rapidly and becomes independent of its parent which soon dies (Fig. 11:9). The root pushes its way into the soil and, branching, develops secondary roots. The first or primary leaf begins the manufacture of starch. The stem becomes eventually the permanent underground stem or **rhizome** from which are later developed more roots and the characteristic leaves or fronds of the fern (Fig. 11:1). Usually only a single sporophyte is formed.

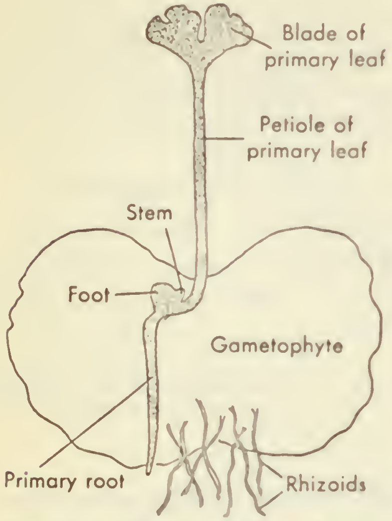

Fig. 11:9 The fern. Young sporophyte (shaded) still attached to, and parasitic upon, the gametophyte. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

(5) SUMMARY OF THE LIFE CYCLE

In the life cycle of a fern (Fig. 11:10) there is an **alternation of generations;** an asexual generation, the sporophyte, which reproduces by means of spores alternates with a sexual generation, the gametophyte, which reproduces sexually by means of gametes. A sporophyte bears sporangia in which spore mother cells give rise to tetrads of spores. A spore develops into a prothallium on which archegonia and antheridia develop, respectively, eggs and sperms. When a sperm unites with an egg a zygote is formed which develops into a new sporophyte.

B. THE FERNS AS A GROUP

There are more than 4000 different species of ferns. They are usually easily distinguished from other plants by their leaves in the form of fronds and their spore-bearing organs. Although widely distributed they reach their greatest luxuriance in the tropics. There large tree ferns 30 to 40 feet in height occur. Great tree ferns and especially large horsetails

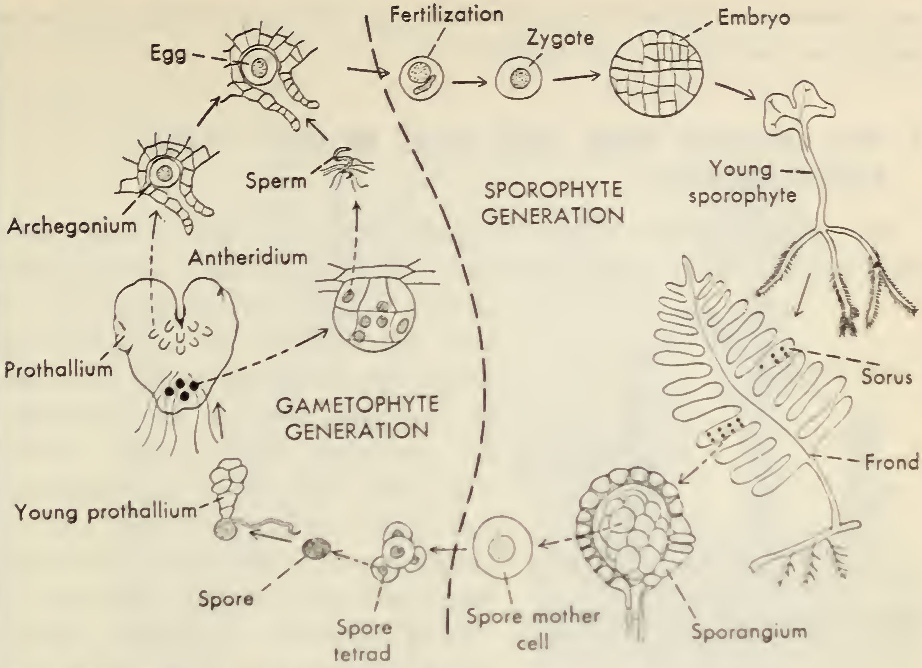

Fig. 11:10 Diagram of the life cycle of a fern.

and club mosses (see below) formed the vast forests of the late Paleozoic era about half a billion years ago before the flowering plants came into existence.

2. THE HORSETAILS (CLASS EQUISETINEAE)

Although differing much in outward appearance (Fig. 11:11) the life history of a horsetail is very similar to that of the fern described. The conspicuous generation is the sporophyte. The sporangia are borne on special leaves or **sporophylls** which occur at the tips of certain of the stems where they are arranged to form cones. The spores, as in the fern, are all of approximately the same size but as is the case in some ferns, they give rise to two kinds of gametophytes, male gametophytes bearing antheridia and female gametophytes bearing archegonia. This may be regarded as a

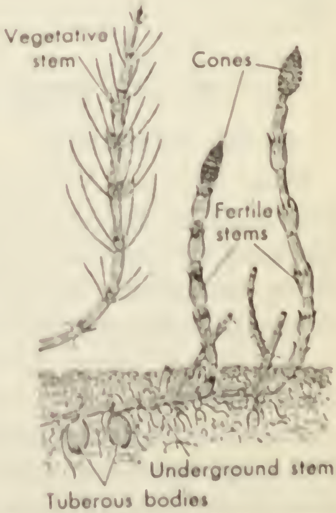

Fig. 11:11 *Equisetum.* Sporophyte. Redrawn from Bergen and Davis, *Principles of Botany,* Ginn and Company.

step toward the differentiation of two types of spores which is seen in some ferns and in the club mosses.

3. THE GROUND PINES AND CLUB MOSSES (CLASS LYCOPODINEAE)

The ground "pines" (genus *Lycopodium*) (Fig. 11:12) are easily confused with the club "mosses" (genus *Selaginella*) but may be distinguished by the shape and arrangement of their leaves. These are needlelike and arranged in spirals round the stem in *Lycopodium* while in *Selaginella* they are arranged in four rows on the stem, two rows of smaller leaves on the upper surface and two rows of larger leaves at the sides. The most important difference is, however, in the life histories, *Lycopodium* producing only one kind of spore while *Selaginella* produces two kinds of spores. The life history of *Selaginella* will be described since it is the more interesting from the point of view of the evolution of the higher plants.

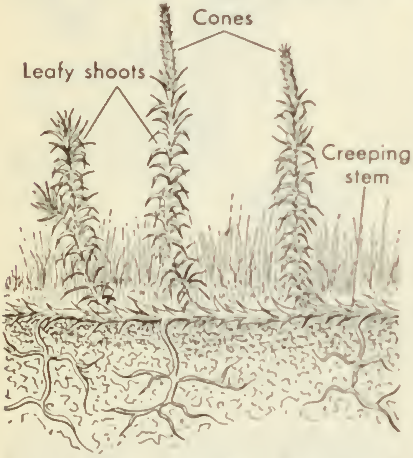

Fig. 11:12 *Lycopodium.* Sporophyte. Redrawn from Bergen and Davis, *Principles of Botany*, Ginn and Company.

A. *THE LIFE CYCLE OF A CLUB MOSS* (SELAGINELLA)

(1) THE SPOROPHYTE

Most species of *Selaginella* are confined to the tropics. Usually there is a much-branched creeping stem and small mosslike leaves. Some species of *Selaginella* seen in greenhouses are relatively large bushy plants, others are small and delicate like a moss. One species is sold in stores under the name of "resurrection moss." In dry weather this plant rolls up into a ball. When the ball is moistened the branches unroll and become green.

The spore-bearing leaves, or sporophylls, form compact **cones** (Fig. 11:13) on the ends of the branches. Each leaf carries a single sporangium but the sporangium is really formed from the stem just above the leaf. Two kinds of spores are produced in the cone, a condition referred to as **heterospory** (Gr. *heteros*, different). One kind, called **microspores** (Gr. *micros*, small), are small and give rise to male gametophytes. The other kind, called **megaspores** (Gr. *megas*, great), are larger and give rise to female gametophytes. The microspores are borne in **microsporangia** on the upper part of the cone while the **megasporangia** occur on the lower part.

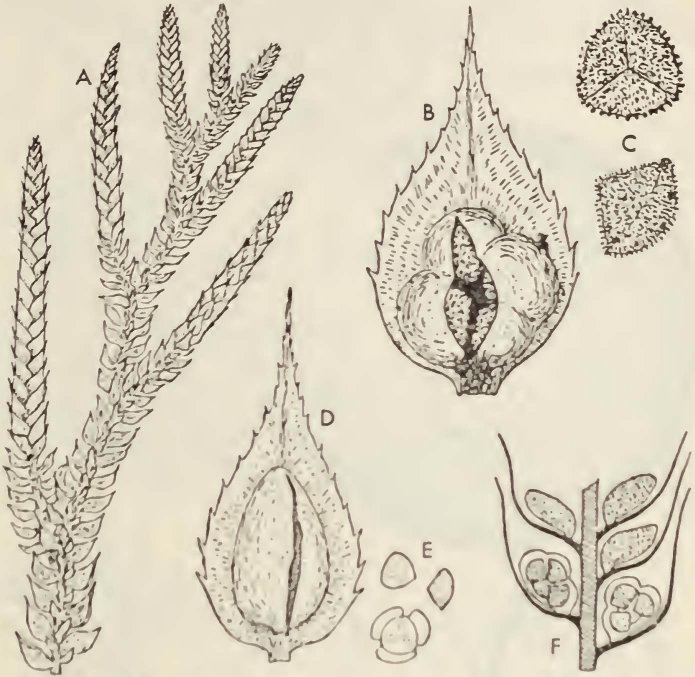

Fig. 11:13 *Selaginella martensii.* A, branch bearing cones; B, inner face of a megasporophyll showing the megasporangium; C, two views of megaspores; D, inner face of microsporophyll showing microsporangium; E, microspores; F, diagram of a longitudinal section of a cone with two megasporophylls below and three microsporophylls above. Reprinted from Bergen and Davis, *Principles of Botany*, Ginn and Company.

(2) THE GAMETOPHYTE

Within the microspore a minute, degenerate, male gametophyte develops. This consists of a single prothallial cell which represents the entire prothallus of a fern and two groups of sperm mother cells which give rise to numerous motile flagellated sperms (Fig. 11:14) which are set free when moisture is available.

The megaspore gives rise to a female gametophyte which begins its development while still in the sporangium and never becomes an independent plant; like the male gametophyte it is a relatively small and degenerate structure. When it is fully developed one end bulges from the spore case. On the exposed surface are a few archegonia (Fig. 11:14) each containing a single egg. Fertilization is possible only when there is sufficient moisture for a sperm to swim to an archegonium. In some cases, however, microspores may fall on the cone in the vicinity of a megasporangium, in which case only a small amount of moisture is required.

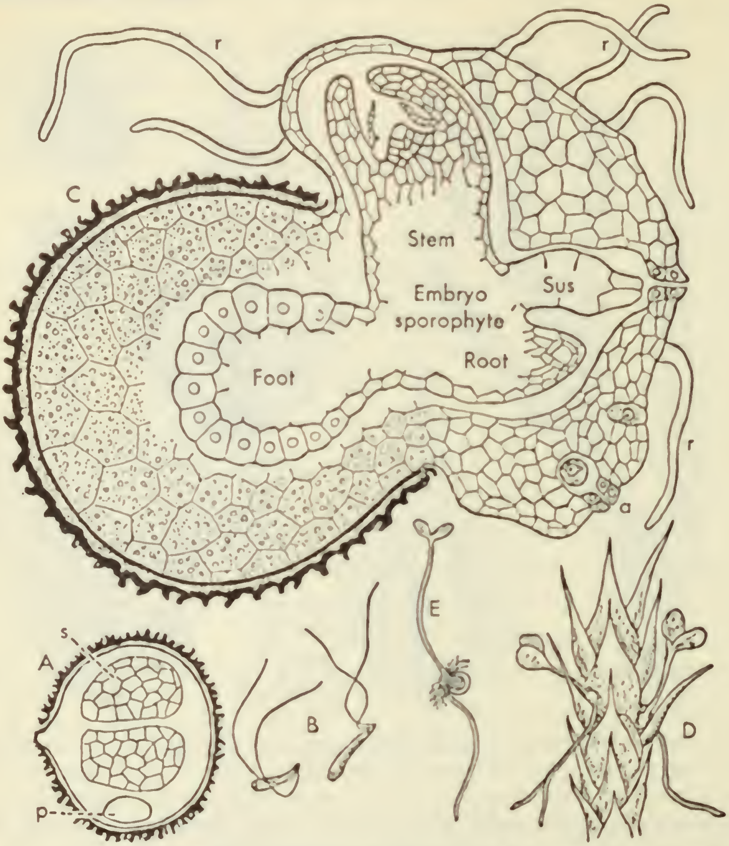

Fig. 11:14 The gametophytes and embryo of *Selaginella*. A, male gametophyte contained within the microspore; *p*, persistent nucleus of prothallial cell; *s*, two groups of sperm mother cells. B, two-ciliated sperms. C, female gametophyte containing an embryo sporophyte; *a*, archegonium; *r*, rhizoids, *Sus*, suspensor. D, young sporophytes held by the spore leaves of the cone. E, a young sporophyte still attached to the megaspore. B, after Balajeff; A, C, D from Miss Lyon. Reprinted from Bergen and Davis, *Principles of Botany*, Ginn and Company.

(3) THE YOUNG SPOROPHYTE

The zygote develops into an embryo sporophyte which begins its development within the female gametophyte (Fig. 11:14) and this may occur even while the latter is still in the sporangium. In addition to the foot, stem, and root of the fern embryo the embryo of *Selaginella* develops a spiral organ called the **suspensor** which forces the young plant down into the tissues of the gametophyte where it obtains protection and nourishment. A suspensor is found in the embryo of the higher plants.

(4) SUMMARY OF THE LIFE CYCLE

The life cycle of *Selaginella* (Fig. 11:15) may be compared with that of a fern, the chief differences being the formation of microspores and megaspores in microsporangia and megasporangia and the degenerate nature of the male and female gametophytes which are dependent on the sporophyte.

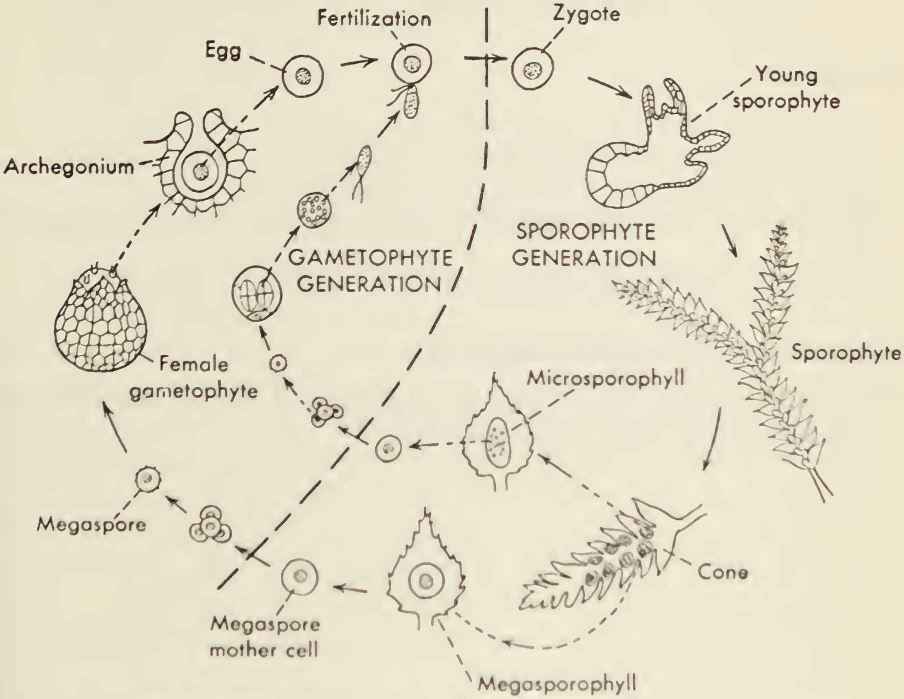

Fig. 11:15 Diagram of the life cycle of *Selaginella*.

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Questions

1. Compare the life cycle of a fern with that of a moss.
2. In what respects is a fern better adapted to life on land than a moss?
3. Compare the life cycle of *Selaginella* with that of a fern.
4. What is heterospory? To what differences in the gametophytes does it give rise?
5. What is the function of the suspensor?

Suggestions for Further Reading

Campbell, Douglas H., *The Structure and Development of the Mosses and Ferns*, The Macmillan Company, New York, 1918.

CHAPTER 12

The Alternation of Generations and Its Significance

1. THE SIGNIFICANCE OF THE ALTERNATION OF GENERATIONS

To survive and be biologically successful a plant must not only be able to grow. It must be able to produce new individuals and ensure that they will find a livelihood. We shall see later that really new individuals are produced only by sexual reproduction. Sexual reproduction to be most effective in producing new individuals involves the union of male and female gametes from different plants — a process called **cross fertilization.** Thus the problem of fertilization must be solved in each species of plant. If a young plant is to survive it must reach a suitable location where it will find the raw materials for the manufacture of its food and not be crowded out by other plants. This is the problem of **dispersal** which must also be solved if the species is to continue. These two problems, fertilization and dispersal, are simplified in the Algae because they live in water. Fertilization is facilitated by either both gametes (*Ulothrix*), or one kind only, the sperm (*Oedogonium*, *Fucus*), swimming through the water. Distribution of the zygotes is aided by water currents.

Both these problems become more complex in the case of a land plant. They are solved by the mosses and ferns by the division of the life cycle into two separate generations and the adaptation of each generation to the solution of one of the problems; the gametophyte looks after sexual reproduction and solves the problem of fertilization while the sporophyte, by producing minute wind-borne spores, provides for distribution. With this division of labor structural differentiation has gone hand in hand, so that the gametophyte is a very different plant from the sporophyte.

The structural differences between the gametophyte and sporophyte generations extend even to the nuclei of their cells. Indeed the nuclear differences probably constitute the most fundamental differences between them. They involve a cycle of changes to which we will now turn

2. THE NUCLEAR CYCLE IN THE ALTERNATION OF GENERATIONS

In a previous chapter (Chap. 4) the complicated process of nuclear division referred to as **mitosis** was described. It will be remembered that in this process certain important structures called **chromosomes** became evident and underwent longitudinal division so that each of the daughter cells came to have the same number of chromosomes and the same kind of chromosomes as the parent cell. This is the usual method of nuclear division and generally occurs whenever cells divide.

A. THE GAMETOPHYTE NUCLEI

When the spore of a moss or fern germinates and develops into a gametophyte, the cells divide in the usual way and the nuclei go through the usual phases of mitotic division. The nuclei of most of the species of ferns which have been investigated contain rather large numbers of chromosomes. However, for the purposes of description we will assume the number in the spore nucleus to be three (Fig. 12:1). When this nucleus divides each of the daughter nuclei contains three chromosomes and the same will be the case in all the cell divisions leading to the mature gametophyte. When the eggs and sperm are formed in the archegonia and antheridia each egg contains three chromosomes and each sperm also three chromosomes.

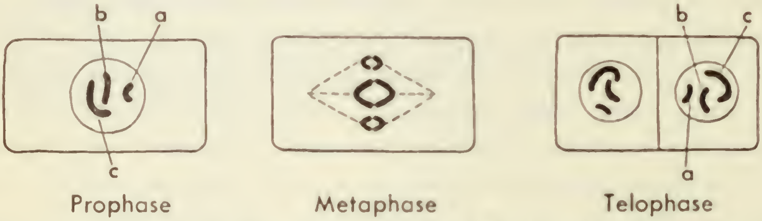

Fig. 12:1 Cell division in the gametophyte of a fern. For the sake of simplicity the number of chromosomes has been assumed to be three. *a*, *b*, *c*, chromosomes.

B. FERTILIZATION

When the sperm and egg unite each brings its three chromosomes to the zygote; in consequence the zygote nucleus has six chromosomes which consist of two corresponding sets of three each (Fig. 12:2). Expressed in another way, while the gametophyte nuclei contain single chromosomes, the zygote nucleus contains pairs of chromosomes (in this case three pairs) one member of each pair being contributed by the male gamete and the other by the female gamete. Two chromosomes which constitute such a pair are said to be **homologous** (Gr. *homos*, the same). Thus the gametes contribute homologous chromosomes.

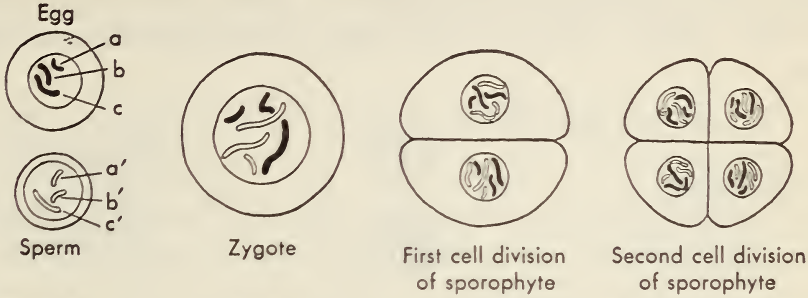
Egg
a
b
c
a′
b′
c′
Sperm
Zygote
First cell division of sporophyte
Second cell division of sporophyte

Fig. 12:2 Nuclear changes in the life cycle of a pteridophyte. Formation of the zygote nucleus by the sperm and egg nuclei and the division of the zygote nucleus to form the nuclei of the cells of the sporophyte. *a*, *b*, *c*, chromosomes of egg. *a′*, *b′*, *c′* chromosomes of sperm.

C. THE SPOROPHYTE NUCLEI

When the zygote divides each of the nuclei of the two daughter cells contains six chromosomes, or three pairs, the zygote nucleus having divided by the usual process of mitosis and each of its chromosomes having divided longitudinally. The same process is repeated during the entire development of the sporophyte.

It has been seen that the difference between the nuclei of the gametophyte cells and those of the sporophyte cells involves more than merely the number of chromosomes. A nucleus which contains only single chromosomes, as is the case in the gametophyte nuclei and the nuclei of the gametes, is termed **haploid** (Gr. *haploos*, simple) while a nucleus which contains pairs of chromosomes, as is the case in the sporophyte nuclei, is termed **diploid** (Gr. *diploos*, double).

D. SPORE FORMATION

Since each spore contains only half the number of chromosomes in a spore mother cell (in the example chosen the spore contains three chromosomes and the spore mother cell six chromosomes) it is clear that the number of chromosomes becomes reduced to half in the process of spore formation. The process by which the number of chromosomes is reduced is called **meiosis**[1] (Gr. *meioun*, to make smaller). Meiosis really consists of two nuclear divisions accompanied by only one division of the chromosomes (Fig. 12:3). Actually the process is somewhat complicated and differs considerably in different cases.

---

[1] The process of meiosis and its relation to the transmission of hereditary characteristics is discussed in more detail in Chap. 37, The Physical Basis of Heredity, and Chap. 38, Heredity.

The nuclear changes in mosses and liverworts are similar to those in the fern; the gametophyte generation is haploid and the sporophyte generation diploid; meiosis occurs when the spore mother cells form spores.

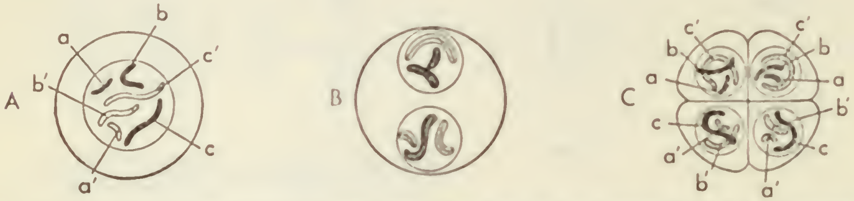

Fig. 12:3 The reduction of the chromosomes during spore formation. A, a spore mother cell in the diploid condition with three pairs of homologous chromosomes. *a*, *b*, *c*, chromosomes of maternal origin; *a'*, *b'*, *c'*, chromosomes of paternal origin. B, the daughter nuclei formed by the first nuclear division. The homologous chromosomes have separated into different nuclei and are dividing longitudinally. C, a tetrad of four spores formed by the second division. The spores differ in the origin of the chromosomes on their nuclei. In two of them the chromosomes are *a*, *b*, and *c'*, in the other two they are *a'*, *b'*, and *c*.

3. THE IMPORTANCE OF THE NUCLEUS

A. THE NUCLEUS IN THE LIFE CYCLE

We have seen that the nuclei of the cells of the gametophyte are haploid while those of the cells of the sporophyte are diploid. This is the basis for regarding the gametophyte and the sporophyte as entirely different plants, both in structure and in mode of reproduction.

B. FERTILIZATION AND REDUCTION

The nuclei of the cells of the gametophyte and of the gametes are haploid. Fertilization leads to the formation of a diploid zygote. The nuclei of all the cells of the zygote, including the spore mother cells, are diploid. The process of meiosis leads to the formation of four haploid spores from each spore mother cell. The haploid spores develop into haploid gametophytes. Thus at fertilization the chromosome number is doubled and at meiosis it is halved.

C. THE REASSORTMENT OF THE CHROMOSOMES

A diploid nucleus contains not only twice the number of chromosomes in a haploid nucleus, but its chromosomes consist of as many pairs of homologous chromosomes as there are single chromosomes in the haploid nucleus. At meiosis the homologous chromosomes are separated, the members of a pair going to different spores. The different spores give rise to gametophytes with different nuclei. The union of gametes from different gametophytes leads to a still further reassortment of the chromosomes in the new zygote (Fig. 12:3).

4. THE DIFFERENTIATION OF THE GAMETOPHYTE AND SPOROPHYTE

Hand in hand with the differentiation of the gametophyte as a sexually reproducing plant, and the sporophyte as an asexually reproducing sporulating plant, has gone a differentiation of the vegetative organs. In the liverworts and mosses the gametophyte is the conspicuous generation, and sporophyte is dependent on it. Nevertheless, the sporophyte does show a considerable amount of differentiation, which is greater in some species than in others. Thus in some mosses, the sporophyte is able to manufacture some of its own food materials, as is seen by the presence of chlorophyll-bearing tissue capable of carrying on photosynthesis in some species. In the ferns the gametophyte is a relatively inconspicuous plant and, although the sporophyte is dependent upon it during its early development, the sporophyte soon becomes independent and the conspicuous generation. The sporophyte of most ferns is a well-differentiated land plant. The rhizome has many of the structural features of the stem of a higher plant, including special conducting tissue. True roots grow out from the rhizome. The fronds, which are true leaves, have an internal structure very similar to the leaves of a seed plant.

The reader is to be cautioned against comparing the gametophyte of a moss with the sporophyte of a fern, e.g., *Lycopodium* or *Selaginella*, which it may superficially resemble. The two plants are fundamentally different, belonging to two different generations. Neither the plants themselves nor any of their organs can be considered homologous.

The gametophyte and sporophyte generations of the bryophytes and pteridophytes have evolved toward a solution of two of the main problems presented to plants by life on land. The gametophyte generation provides for cross-fertilization, although water is still necessary for the union of the gametes. The sporophyte generation provides for distribution.

We shall find that this trend, already evident in passing from the bryophytes to the pteridophytes, in which the gametophyte becomes the inconspicuous, and the sporophyte the more conspicuous generation, is carried further in the seed plants, where what is ordinarily called "the plant" with its roots, stem, and leaves is the sporophyte generation, while the gametophyte generation is a minute, entirely dependent, organism involved in the formation of the seed (Fig. 14:15).

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Questions

1. What is the essential biological difference between asexual and sexual reproduction?
2. Describe the nuclear changes in the life cycle of the fern.
3. Explain how the processes of reduction and fertilization lead to a reassortment of the chromosomes.
4. Discuss the significance of an alternation of generations.

CHAPTER 13

Seed Plants (Phylum Spermatophyta), The Gymnosperms (Class Gymnospermae), Life Cycle of the Pine

In the case of the seed plants or Spermatophyta (L. *sperma*, seed) the plants we see are the sporophytes, the gametophytes having become reduced to minute stages which never become independent plants. Two kinds of spores are produced by the sporophyte: **microspores** which germinate into male gametophytes, also called **pollen grains,** and **megaspores** which germinate into female gametophytes. The female gametophyte undergoes its relatively simple development while still within the sporangium, which in this case forms part of a structure called an **ovule;** there the egg is fertilized and there a young sporophyte, at first called an **embryo,** begins its development. While the formation of the embryo is in progress the tissues of the female gametophyte and of the ovule become modified to form around it a protective covering. Then the development of the embryo is arrested and the whole structure becomes a seed. A **seed** may be defined as a ripened ovule, or since an ovule is practically equivalent to a sporangium, it may be regarded as a sporangium in which an embryo has formed.

Spermatophytes are divided into two groups or classes: the Gymnospermae and the Angiospermae. The gymnosperms include most of our evergreens. The angiosperms include all flowering plants. We will consider first the gymnosperms which are the more primitive.

The class Gymnospermae includes the interesting tropical plants called **cycads,** which are among the most primitive of seed plants, and the conifers, which form great forests and provide most of the lumber used in the United States. The name Gymnospermae means "naked seeds" and refers to the fact that the seeds of these plants are not enclosed as are those of the flowering plants (Angiospermae). Our most familiar gymnosperms are the coniferous trees such as the pine, spruce, fir, hemlock, redwood, juniper, cedar, larch, and cypress.

I. THE LIFE CYCLE OF THE PINE

A. THE SPOROPHYTE

The sporophyte of the pine like that of most gymnosperms is an evergreen tree. It is "evergreen" because its leaves are not shed in the autumn. The length of time which the leaves remain on the tree varies from two to ten years with the species and the locality. The following description applies more particularly to the white pine. The main stem or tree trunk is straight and vertical. The branches grow out horizontally, the older and larger ones being nearest to the ground. This gives to the whole tree when growing in the open the shape of a large inverted cone. The method of branching in which the main stem continues its growth vertically and the branches grow out horizontally is termed **excurrent.** An excurrent mode of branching is characteristic of most gymnosperms. A peculiarity of pine is its long slender leaves, called **needles,** which are grouped together on the branches in clusters of from two to five (Fig. 13:1).

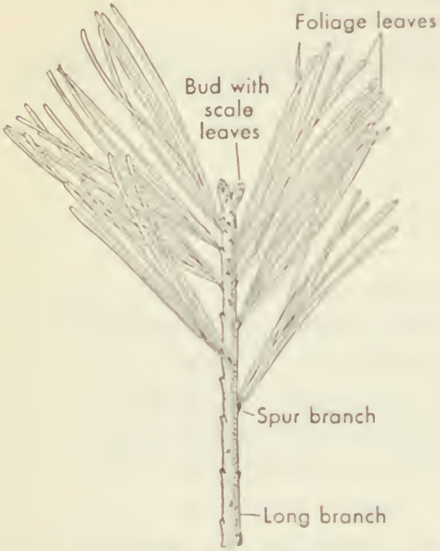

Fig. 13:1 White pine. Apical portion of the stem. Note the spur branches, each bearing five foliage leaves. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

B. SPORE FORMATION

Like the club moss, *Selaginella*, described in the chapter on the Pteridophytes, the pine is **heterosporous,** i.e., bears two kinds of spores. One kind, the **microspores,** which are small and produce male gametophytes, are called **pollen grains.** The other kind, the **megaspores,** are larger and produce female gametophytes. The spore-bearing leaves or sporophylls are scalelike and arranged on the ends of short branches forming the familiar pine cones or **strobili** (singular, **strobilus**). The microspores and megaspores are produced on the same tree but in different cones.

The cones which bear the microspores (Fig. 13:2 A) are called

staminate cones because they produce pollen like the stamens of a flower to which they correspond.

The name pollen grain is commonly applied to the microspore and to the early stages of the male gametophyte which develops while the microspore is still in the sporangium. This sporangium, since it bears the microspores, is called a **microsporangium.** The scalelike leaves of the cone, which bear the microsporangia, are called **microsporophylls,** or, following out the comparison with a flower, they may be called **stamens.** Each microsporophyll bears two microsporangia on its under side (Fig. 13:2 B, C). The microsporangia at first contain numerous microspore mother cells, the nuclei of which contain the diploid number of chromosomes. Each microspore mother cell divides to form four haploid microspores or pollen grains. The staminate cones occur in clusters near the ends of the long branches and appear in the late spring

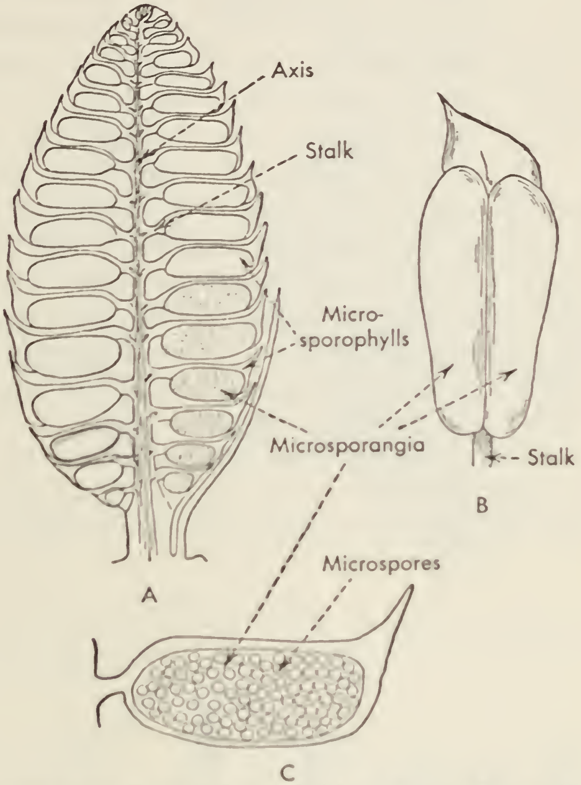

Fig. 13:2 Staminate cone of pine. A, longitudinal section; B, ventral view of microsporophyll; C, section of microsporophyll. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

toward the end of the growing season. After a few weeks the pollen is shed and the cones wither and drop off.

The cones which bear the megaspores are called **carpellate** cones (Fig. 13:3) because their scales correspond to the carpels or seed-bearing leaves of a flower. These cones occur on the ends of the longer branches and appear about the same time as the staminate cones. Each scalelike **megasporophyll** or **carpel** bears two **megasporangia** on its upper side (Fig. 13:4, A). Each megasporangium contains a single megaspore mother cell which divides to form four megaspores. As in the case of the microspore development the nucleus of the megaspore mother cell contains the diploid number of chromosomes while the nucleus of a megaspore is haploid. Usually only one of the megaspores develops into a gametophyte.

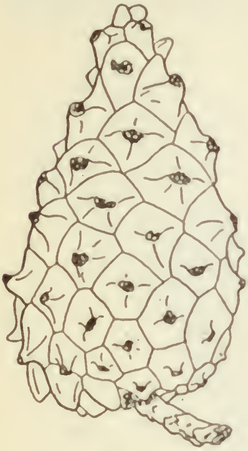

Fig. 13:3 A carpellate cone of pine.

The megasporangium of the pine, called also the **nucellus**, differs from that of the fern by being enclosed in an **integument**. The integument entirely encloses the nucellus except for a small opening called the **micropyle** (Fig. 13:5 B). The nucellus with its enclosing integument is

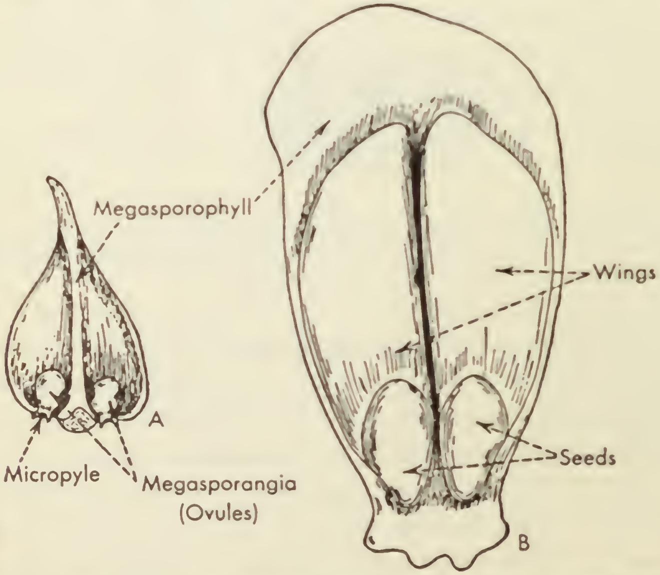

Fig. 13:4 Megasporophyll of pine viewed from the side which is uppermost in the young cone. A, about the time of pollination; B, after the seeds have matured. The two drawings have been made from different species. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

called the **ovule** and corresponds to the structure of the same name in the flower. The megasporangium contains only one megaspore mother cell (Fig. 13:5 B). This divides by reduction division forming four cells with haploid nuclei, one of which grows larger than the others and becomes the single functional megaspore, while the other three degenerate.

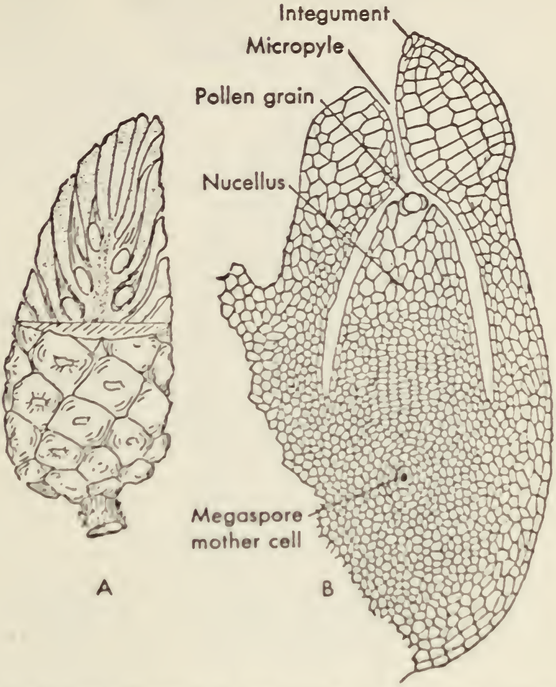

Fig. 13:5 Carpellate cone of pine in section. A, entire cone, upper part in section; B, longitudinal section of a megasporophyll. After Bessey from Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

C. THE FEMALE GAMETOPHYTE

The megaspore germinates while still in the nucellus or megasporangium. However, the megaspores formed during the spring of one year do not begin to germinate until the following spring. The **female gametophyte** which develops from the megaspore remains small and entirely dependent on the sporophyte. Its cells differ from those of the surrounding nucellus by being haploid, while the cells of the nucellus have the diploid number of chromosomes of all sporophyte cells. The female gametophyte never develops chlorophyll but grows at the expense of the nucellus by absorbing nourishment from it. Toward the end of the summer, the second after the formation of the megaspore, two or three **archegonia** are formed in the female gametophyte at the end near the micropyle (Fig. 13:6). Each archegonium consists of a single large **egg cell** and several small **neck cells**.

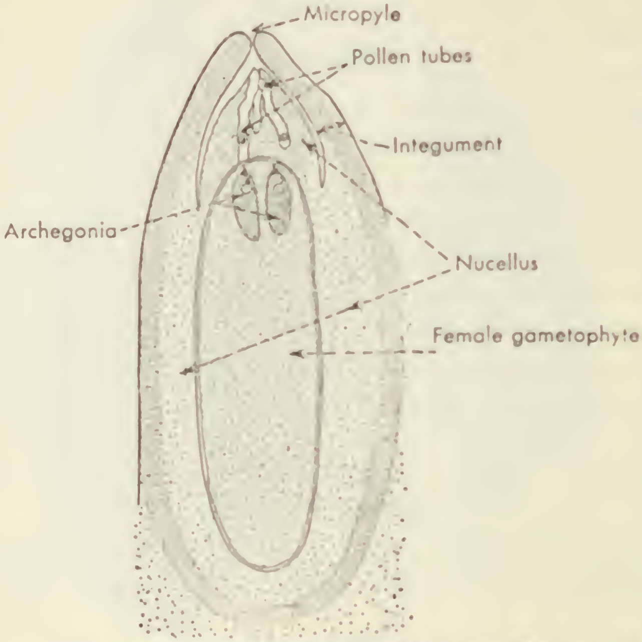

Fig. 13:6 Ovule of pine at about time of fertilization. After Coulter and Chamberlain, *Morphology of the Gymnosperms*, from Holman and Robbins, *Textbook of General Botany*, by permission of the University of Chicago Press and John Wiley & Sons, Inc.

D. THE MALE GAMETOPHYTE

The male gametophyte starts to develop while the pollen grain is still in the microsporangium. The single cell of the microspore (Fig. 13:7 C) divides within the spore wall into two cells of unequal size. The smaller of these is called the **first vegetative cell** (Fig. 13:7 D). The larger cell divides again unequally, forming a smaller **second vegetative cell** and a larger **antheridial cell** (Fig. 13:7 E). The first and second vegetative cells soon degenerate and become disorganized. They appear to represent the extensive tissue of the gametophyte of a fern but in the pine to be without function. The antheridial cell divides to form a smaller **generative cell** and a larger **tube cell** (Fig. 13:7 F). It is in this stage that the pollen grain, now containing an immature male gametophyte, is shed. Further development of the male gametophyte depends upon its reaching a carpellate cone.

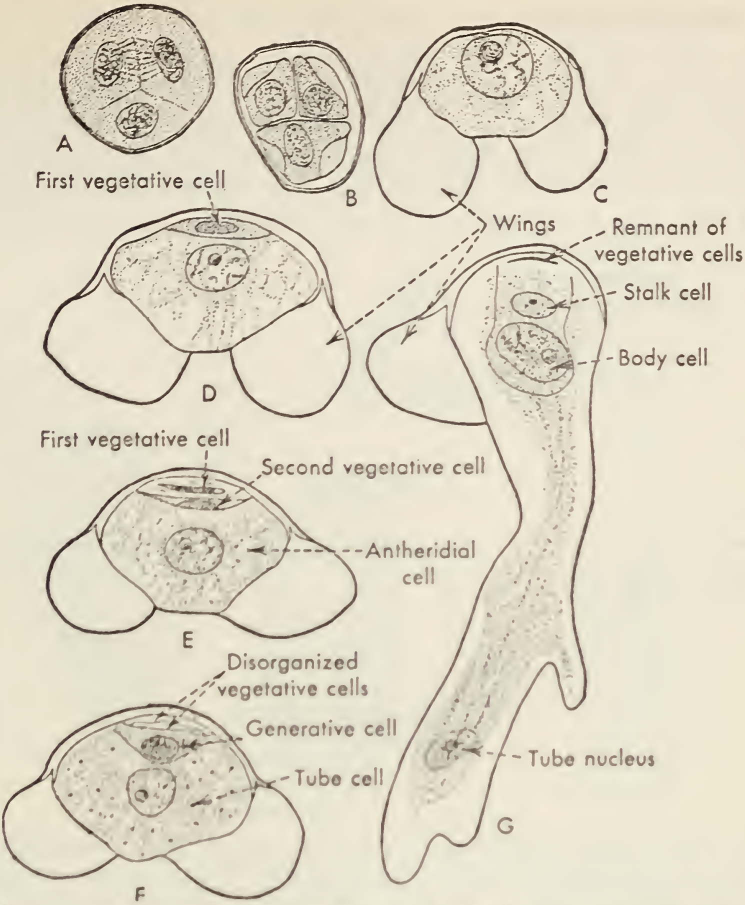

Fig. 13:7 Successive stages in the development of the microspore and male gametophyte of *Pinus laricio*. A, the telophase of the second division of the spore mother cell; B, three of the four spores of a tetrad some time before maturity; C, a mature microspore; D to F, successive stages in the development of the male gametophyte up to the time the spores are shed; G, the male gametophyte about a year after pollination and some time before fertilization. After Coulter and Chamberlain, *Morphology of the Gymnosperm*, from Holman and Robbins, *Textbook of General Botany*, by permission of the University of Chicago Press and John Wiley & Sons, Inc.

E. POLLINATION

Toward the end of spring when the pine trees are shedding their pollen in yellow clouds, the air is loaded with the fine grains. Inevitably some of these fall between the scales of the carpellate cones near the micropyle of an ovule. From the region of the micropyle the ovule secretes a watery liquid which serves to catch the pollen. As this liquid evaporates, the pollen is drawn through the micropyle into a space between the integument and the nucellus called the **pollen chamber**.

F. FERTILIZATION

Shortly after the pollen grains arrive in the pollen chamber they begin to develop **pollen tubes** (Fig. 13:7 G), but their development is retarded until the following spring. The tube cell grows through the tissue of the nucellus toward the female gametophyte and arrives there at about the time the egg cells are developed in the archegonia. As the pollen tube grows in length the tube nucleus moves into its tip and the generative cell divides into a **stalk cell** and a **body cell** (Fig. 13:7 G) which also pass into the pollen tube. The nucleus of the body cell then divides forming two **sperm nuclei.** When the pollen tube has penetrated the neck of an archegonium and reached an egg cell, the end bursts and liberates the contents into the cytoplasm of the egg. One of the sperm nuclei unites with the egg nucleus and the rest of the tube contents degenerate and disappear. The nuclear divisions, which occur in the development of the male gametophyte up to the time of fertilization, are shown in Fig. 13:8.

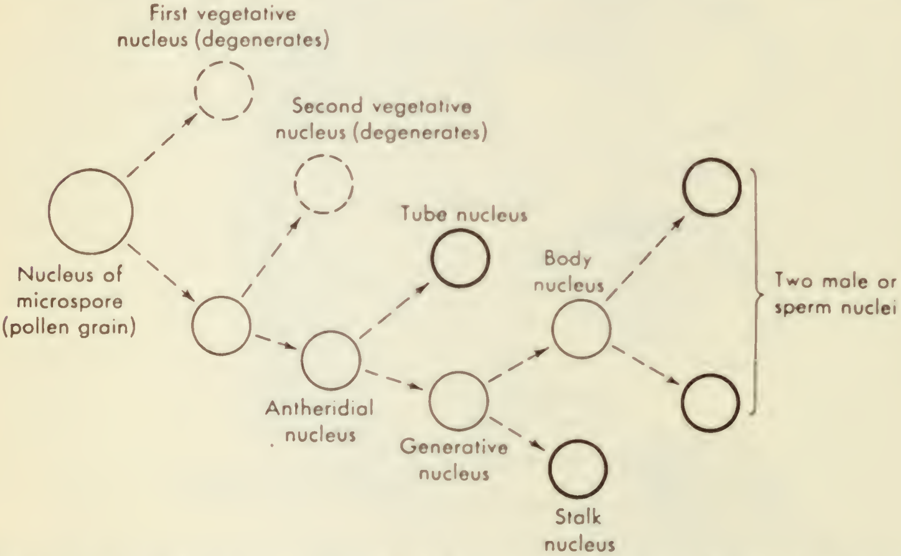
First vegetative nucleus (degenerates)
Second vegetative nucleus (degenerates)
Tube nucleus
Body nucleus
Two male or sperm nuclei
Nucleus of microspore (pollen grain)
Antheridial nucleus
Generative nucleus
Stalk nucleus

Fig. 13:8 Pine. Nuclei formed during the development of the male gametophyte from a microspore. Vegetative nucleus is equivalent to nucleus of vegetative cell. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

G. THE DEVELOPMENT OF THE SEED

The zygote begins immediately to develop into an embryo. The nucleus divides first into two and then into four nuclei. These four nuclei then move to the lower portion of the egg where each divides again. This time, however, cell walls are formed so that eight cells result. By further cell divisions a total of sixteen cells is produced. From the lower cells, i.e., those farthest from the neck of the archegonium, one or a number of embryos begin to develop. However, in the pine all except one of these embryos usually die.

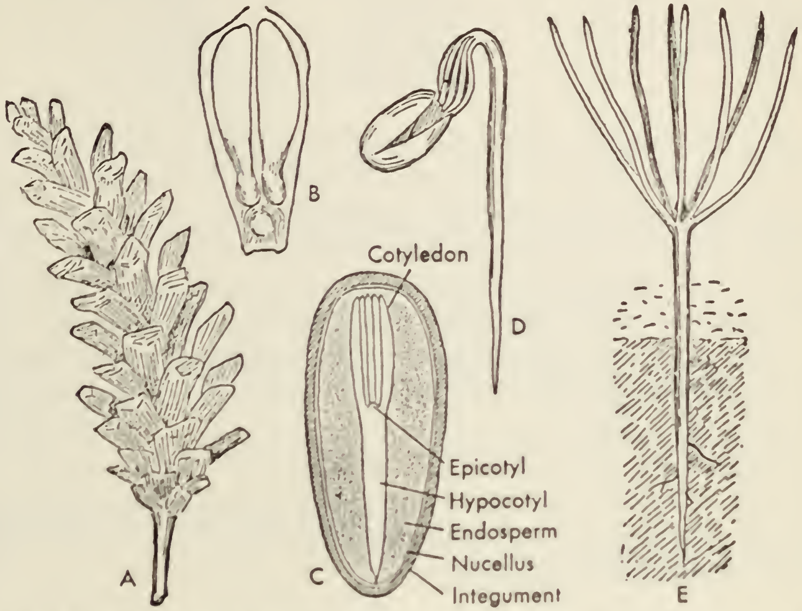

Fig. 13:9 Pine. A, carpellate cone at time seeds are shed; B, scale with two seeds; C, longitudinal section of seed (the female gametophyte has become the endosperm); D, E, germination of a seed. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

While the zygote is undergoing its early development into an embryo sporophyte, the ovule and its contents become transformed into a seed. The female gametophyte grows at the expense of the nucellus (megasporangium) which becomes reduced to a thin layer under the integument of the ovule, which latter now becomes the integument of the seed (Fig. 13:9). The integument of each seed develops a winglike appendage. In a ripe seed the embryo occupies the central position. The embryo usually bears six to eight seed leaves or **cotyledons** which are arranged in a ring around one end of a central axis. The part of this axis below the cotyledons is called the **hypocotyl** while the small part above is called the **epicotyl**. The cells of the female gametophyte take up reserve food materials and become the **endosperm**. The seed of the pine thus consists of an integument surrounding the remnant of the nucellus which in turn surrounds the endosperm in the center of which is the embryo. The generations to which these parts of the seed belong are shown in the table:

TABLE 13:1. THE PARTS OF A PINE SEED AND THE GENERATIONS TO WHICH THEY BELONG

STRUCTURE	GENERATION	CHROMOSOME NUMBER
Integument	Sporophyte	Diploid
Nucellus (megasporangium)	Sporophyte	Diploid
Female gametophyte	Gametophyte	Haploid
Embryo	Sporophyte	Diploid

During the development, which begins with pollination and culminates with the formation of the seed, the scales of the carpellate cone are tightly pressed together. Soon after pollination the stalks of the carpellate cones which up to this time have held the cones erect on the tree, change in their reaction to gravity. Growth on one side is more rapid than on the other so that the stalk bends over causing the cone to hang down. The scales separate when the seeds become ripe and allow the latter to fall to the ground. The winglike appendage of the seed aids its dispersal by the wind.

The seeds of the pine usually do not germinate until the spring after they have left the cone. If at the end of this time they have reached moist ground the radicle grows out and is forced into the ground by the elongation of the hypocotyl (Fig. 13:9).

2. OTHER GYMNOSPERMS

The pine which has just been described is a member of the order Coniferales. From the point of view of evolution the cycads, order Cycadales, are of special interest. The sporophyte of these plants resembles a palm. The life cycle more nearly resembles the pine. As in the pine, microspores and megaspores are borne on staminate and carpellate cones, but the two kinds of cones are borne on different plants. The pollen from the male plant is transferred to the carpellate cones of a female plant by air. Of particular interest is the fact that the male gametophyte which develops from the pollen grain contains several cells and that in the pollen tube two motile sperms are developed and swim to the egg cell, indicating how the evolution from the motile sperm of the pteridophytes to the nonmotile sperm nuclei of the pine and the flowering plants may have occurred.

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Questions

1. Compare a pine tree with the sporophyte of a fern and with the sporophyte of *Selaginella.*
2. Compare the cones of a pine with the cone of *Selaginella.*
3. To what structures in *Selaginella* does the seed of the pine correspond? Compare the two corresponding stages in the life cycle.
4. In what ways is the pine better adapted to life on land than any of the Pteridophytes?
5. Describe a pine seed indicating the nuclear condition of each part.

Suggestion for Further Reading

Coulter, J. M., and C. J. Chamberlain, *Morphology of the Gymnosperms*, University of Chicago Press, Chicago, 1903.

CHAPTER 14

Seed Plants (Phylum Spermatophyta), The Angiosperms (Class Angiospermae), Life Cycle of a Flowering Plant

The greater part of the earth's vegetation consists of flowering plants. However, in many cases the flowers are inconspicuous. The scientific name of the class refers to the fact that the seeds which contain an embryo sporophyte are enclosed in a seed case. This and other features which will be described have enabled this group of plants to adapt themselves to life under a great variety of conditions. They represent the highest level to which plant evolution has yet attained.

1. GENERAL ACCOUNT OF LIFE CYCLE

A. THE PLANT BODY

The plant with which we are familiar represents the sporophyte generation, the gametophytes being microscopic plants dependent on the sporophyte throughout their existence. It is convenient to begin with the sporophyte. Almost any plant could be made to serve the purposes of a general description. We have chosen the sunflower.

The sunflower plant is composed of a shoot and a root (Fig. 14:1). The **shoot** consists of the **stem** and **leaves** and grows upward into the air, while the **root** grows downward into the ground. The stem is divided into **nodes** and **internodes.** The nodes are the slightly enlarged portions of the stem where the leaves arise. They are separated by the internodes. In the sunflower the leaves arise singly, one at a node. Such an arrangement is said to be **alternate.** When two leaves arise at each node, opposite to each other, the arrangement is said to be **opposite.** When a number of leaves arise at a node equally spaced around it the arrangement is called a **whorl.** A leaf consists of a flat portion or **blade** and a stalk or **petiole** by which it is attached to the stem. The upper angle between the petiole and the stem is called the **leaf axil.** At the tip of the stem is the "flower," which in the sunflower is really a cluster of small flowers. The root consists of a main portion or **primary root** extending vertically downward, from which **branch roots** extend.

The leaves, stem, and roots are plant organs. They are specialized to perform different functions in the life of the plant. The functions of the leaves are to manufacture carbohydrates (photosynthesis) and nitrogenous food materials and to give off water (transpiration). The functions of the stem are to support the leaves and expose them to the sunlight, to conduct water and mineral salts from the roots to the leaves, and to conduct a portion of the food materials manufactured in the leaves to the roots. In the sunflower the stem contains some chlorophyll and is therefore able to aid in the manufacture of food materials. The functions of the roots are to anchor the plant in the ground so that the stem is maintained in an upright position, and to absorb water and mineral salts from the soil. Another function which is often taken on by roots, stems, or leaves is that of food storage.

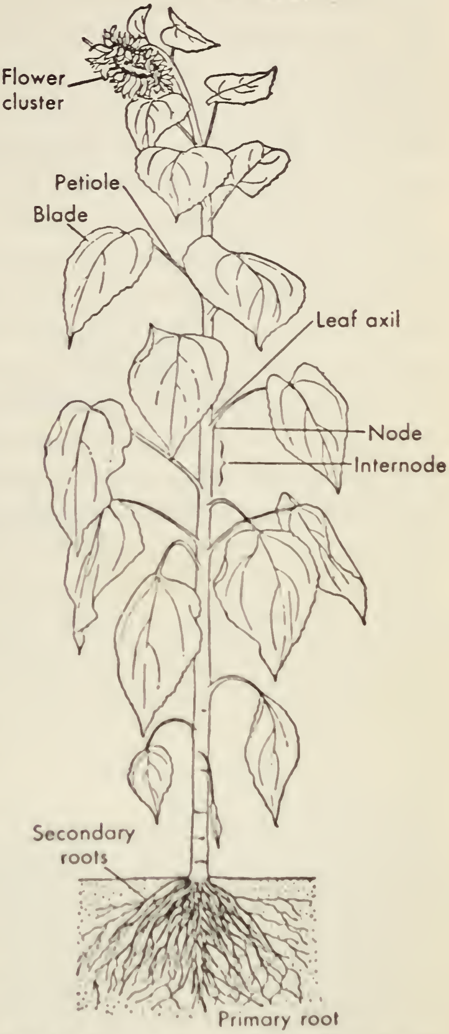

Fig. 14:1 A sunflower plant. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The stem of the sunflower is composed mainly of soft tissue. When deprived of water the whole plant dries up or wilts. In the winter the stem dies and withers. Such plants are called **herbs** and the sunflower is said to be an "herbaceous plant." Indian corn and wheat are other examples of herbaceous plants. They are to be contrasted with **trees** and **shrubs** which have woody stems and do not die in the winter.

The sunflower plant lives for only one season. After blooming and forming seed, it dies. New plants grow from the seed the next spring. Such a plant is said to be an **annual**. Other examples of annuals are corn and wheat. In other herbaceous plants, for example, the beet or turnip, the shoot produces no flowers during the first year, all of its activity going to the storage of food materials in the root which does not die as the shoot does at the end of the summer. Next spring a new shoot grows from the old root and produces flowers and seeds after which the whole plant dies. Such plants which live for two years are called **biennials.** In other herbaceous plants food materials may be stored under ground from year to year so that a succession of flowering shoots may be produced each year. These are **perennial herbs;** examples are asparagus, rhubarb, dahlia, and gladiolus. Trees and shrubs are woody perennials.

The stem of a plant is by no means always **erect.** It may lie along the ground and be **prostrate** as in the strawberry and watermelon, or it may be actually **underground** as in the case of many grasses. On the other hand a stem may twine around the stems of other plants as in many climbing plants, e.g., the bean and grape. The erect stems of trees are of two principal types. The **excurrent type** of stem is illustrated by the white pine, in which the main stem grows vertically while the branches grow out horizontally. It is the common type in conifers but occurs only rarely in angiosperms. The **deliquescent type** is illustrated by the elm in which there is usually no one main stem and the branching is irregular.

The leaves of plants vary greatly in form and structure. They may be divided into **vegetative leaves** which have to do with the metabolism and growth of the plant and **floral leaves** which make up the flower and function in the reproduction of the plant. Vegetative leaves may take the form of ordinary green **foliage leaves, scale leaves** such as those which protect the buds, or **bracts** — small leaves in the axils of which flowers are borne.

Perennial woody plants like trees and shrubs carry on their growth mainly during the spring and summer. New branches and leaves are formed from the **buds** which lie dormant during the winter. Buds occur usually at the ends of branches or in the axils of leaves. When at the end of a branch a bud is said to be **terminal.** When in the axil of a leaf it is called an **axillary bud.** Occasionally buds occur at other points on the stem when they are called **adventitious buds.** Buds may give rise to branches and foliage leaves only, branches, foliage leaves, and flowers, or flowers only.

B. THE FLOWER

Flowers are essentially reproductive organs specially adapted to reproduction on land. The entire gametophyte generation which in the mosses and ferns is represented by separate and independent plants is crowded into the flower and concealed from the casual observer whose attention is held by the delicate beauty of the often highly colored petals or sepals which are not essential to the reproductive processes.

There are many types of flowers, some of which like those of the grasses and many trees are inconspicuous and lacking in distinctive coloration. A little study soon shows that all flowers are in reality whorls of modified leaves borne on the ends of stems or branches in which the internodes or stretches between the leaves are shortened so that the separate whorls are close together and appear to be one within the other.

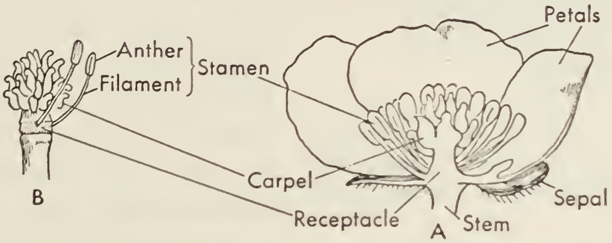

Fig. 14:2 The buttercup, *Ranunculus*. A, a flower divided longitudinally; B, a flower from which the sepals, petals, and all but two stamens have been removed. After Francis Darwin, *Elements of Botany*, Cambridge University Press.

DESCRIPTION OF A SIMPLE FLOWER

The structure and significance of the flower can best be approached by studying a relatively simple flower such as that of the buttercup (Genus *Ranunculus*). The end of the stem on which the flower is borne is called the **receptacle** (Fig. 14:2). The outer whorl which is composed of five small, pointed, yellowish green leaves, called **sepals,** is the **calyx.** Within the calyx is the whorl of five larger yellow leaves called **petals** which make up the most conspicuous part of the flower and form the **corolla.** The petals alternate with the sepals, that is, they occupy the spaces between them. The term **perianth** is applied to the sepals and petals collectively. Passing inward we come next to a number of whorls of small filamentous bodies called **stamens.**

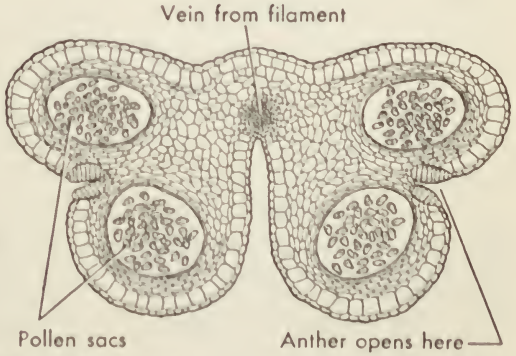

Fig. 14:3 Cross section of the anther of a lily. Redrawn from Bergen and Davis, *Principles of Botany*, Ginn and Company.

When magnified, each stamen is seen to consist of a **filament** which bears on its free end an enlargement, the **anther.** A cross section of an anther shows cavities; two on each side of the attachment of the filament (Fig. 14:3). These cavities are really the cavities of four sporangia. The spores produced in these sporangia are commonly called **pollen grains** but they may also be called **microspores.** While still in the pollen sac the pollen grain or microspore, which is at first a single cell, divides within its outer coat or spore wall to form a much-reduced male gametophyte. As in the fern and other pteridophytes and bryophytes, the formation of spores is preceded by spore mother cells, in this case called **microspore mother cells.** Two cell divisions, in one of which there is a reduction division of the nucleus, lead to the formation of tetrads of spores as in the ferns. It now becomes evident that the stamens are sporophylls and can be compared to leaves. When this is done, the filament is found to correspond to the petiole and the anther to the blade which in this case bears four sporangia. That the stamens really correspond to leaves is seen in the flower of the white water lily (Fig. 14:4), where there is a gradual transition from petals to stamens. In some of the common cultivated varieties of the geranium and nasturtium the filaments of the stamens may develop leaflike outgrowths.

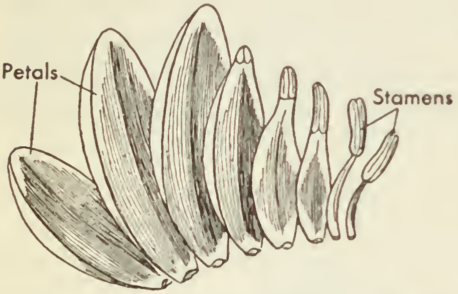

Fig. 14:4 Transition from petals to stamens in the white water lily. Redrawn after Asa Gray, *Structural Botany*, The Macmillan Company.

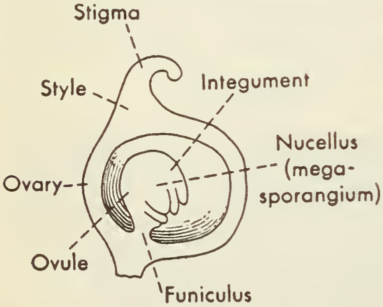

Fig. 14:5 Ovary of buttercup, divided lengthwise to show the single ovule. After Asa Gray, *Structural Botany*, The Macmillan Company.

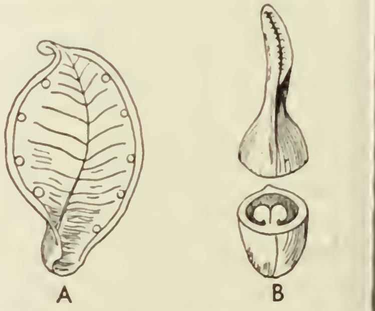

Fig. 14:6 A leaf incurving to show the morphology of a simple pistil. A, leaf incurving; B, pistil cut across to show ovules. Redrawn after Asa Gray, *Structural Botany*, The Macmillan Company.

In the center of the flower, bunched together but nevertheless in whorls, are the **carpels.** These small, green, pointed, oval bodies are even less like leaves than the stamens (Fig. 14:5). However, a carpel is merely a small leaf with its lateral margins bent around and fused together so as to form a little sac enclosing a cavity (Fig. 14:6). In the buttercup the carpels remain separate, giving rise to a condition which is called **polycarpous.** The small sac formed by the folding over of the margins of the carpels is called an **ovary** and the cavity of the sac a **locule.** Projecting into the ovary [1] and occupying a considerable amount of the cavity is an **ovule** (Fig. 14:5). The carpels, like the stamens, are sporophylls. The spores which are produced in the ovules are, however, quite different from pollen grains. They are called **megaspores** and give rise to female gametophytes.

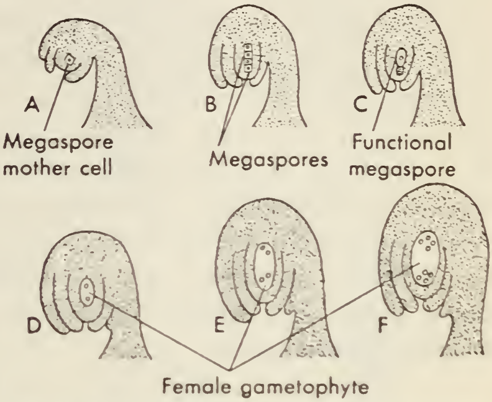

Fig. 14:7 Longitudinal section of ovule showing the development of the megaspores and female gametophyte of an angiosperm. A, single megaspore mother cell; B, megaspore mother cell has given rise to four megaspores; C, the megaspore farthest from the micropyle enlarges and becomes the functional megaspore; D, first division of megaspore nucleus in development of the female gametophyte; E, female gametophyte with four nuclei; F, female gametophyte with eight nuclei. Redrawn after Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The ovule of a flower is attached by a stalk or **funiculus** to the ovary, the place of attachment being called the **placenta.**[2] The ovule consists of a **megasporangium,** called also a **nucellus,** and an **outer** and an **inner integument** which are formed as outgrowths from the base or attached end of the sporangium and do not quite meet over the other end, leaving an opening, the **micropyle** (Fig. 14:5). Only a single **megaspore mother cell** is formed in the megasporangium. This gives rise usually to four megaspores only one of which, that farthest away from the micropyle, becomes functional, i.e., develops into a greatly reduced female gametophyte (Fig. 14:7, a, b, c).

At the pointed, hooklike, upper end of each carpel is an organ called the **stigma,** which is specially adapted to receive the pollen. In most flowers the stigma is borne upon a stalk called the **style.** The ovary, style

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[1] Unfortunately the older botanists imagined a parallel between this part of a flower and the female reproductive organ of an animal — a parallel which has no foundation in anatomy.

[2] The use of the word "placenta" in this connection should not be confused with its use for the attachment of the embryo to the uterus in mammals.

(when present), and stigma constitute the **pistil.** In many flowers the carpels fuse to form a single axial body called a compound pistil. The carpels are then said to be syncarpous.

The microspores begin their development into male gametophytes while still within the pollen sacs and the megaspores not only begin but complete their development in the ovule. Further, the formation of the seed requires that the pollen grains be transported to the stigma. These conditions create a rather interesting situation. Although the sporophyte does not reproduce sexually, nevertheless the fact that it produces two kinds of spores which develop into male and female gametophytes respectively is, as it were, reflected back into its structure so that we can in a way think of the stamens as male organs and the carpels as female organs of reproduction. The sepals and petals protect the stamens and pistils and attract insects to the flower. Because the sepals and petals are not directly concerned with reproduction they are called **accessory floral parts.** The stamens and pistils, on the other hand, are called **essential floral parts.**

C. THE FEMALE GAMETOPHYTE

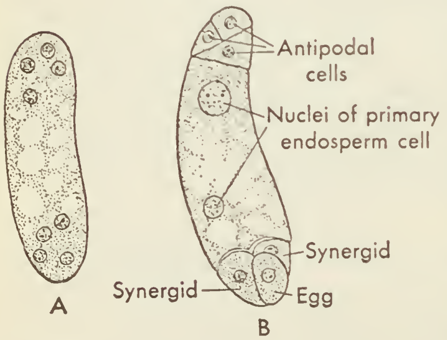


Fig. 14:8 The female gametophyte of a flowering plant. A, stage with eight nuclei, four at either end, and no division of the cytoplasm; B, mature female gametophyte. Redrawn from Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The female gametophyte, also referred to as the embryo sac, undergoes its development within the nucellus or megasporangium. The single nucleus divides into two, four, and eventually eight daughter nuclei without any accompanying division of the cytoplasm. These eight nuclei are arranged in the gametophyte so that four are at the end near the micropyle and four at the opposite end (Fig. 14:8 A). From each of these groups of four nuclei, one nucleus called a **primary endosperm nucleus** moves toward the center of the gametophyte (Fig. 14:8 B). The cytoplasm now becomes divided by cell walls. At the micropylar end three cells are formed, each with a single nucleus. One of these is the single **egg cell** while the other two are called **synergids,** and are believed by some to correspond to a much reduced archegonium. At the opposite end three **antipodal cells** are formed. The cytoplasm occupying the central portion of the gametophyte and surrounding the two endosperm nuclei becomes a large two-nucleated cell, the **primary endosperm cell.** This simplified structure consisting of eight nuclei divided among seven cells and containing a single egg is the mature female gametophyte of a flowering plant.

D. THE MALE GAMETOPHYTE

The development of the microspores or pollen cells begins while they are still in the pollen sac (Fig. 14:9 A, B). The first division of the microspore cell leads to the formation of a **generative cell** and a **tube cell.** (It will be noticed that the cell divisions leading to the formation of vegetative cells which occur in the pine are omitted in the development of the male gametophyte of the flowering plant.) In most flowering plants the pollen grains are liberated from the pollen sacs at this stage and further development does not take place unless the pollen grain is carried to the stigma either of the same flower or another flower of the same species. When this occurs, the tube cell grows out as a **pollen tube** (Fig. 14:9 C). The pollen tube elongates rapidly, growing down through the tissues of the stigma and style to the ovule. First the tube nucleus and then the generative cell migrate into and down the pollen tube (Fig. 14:9 D). The nucleus of the generative cell divides to form two male gamete nuclei or **sperm nuclei,** either before or after it has moved into the pollen tube.

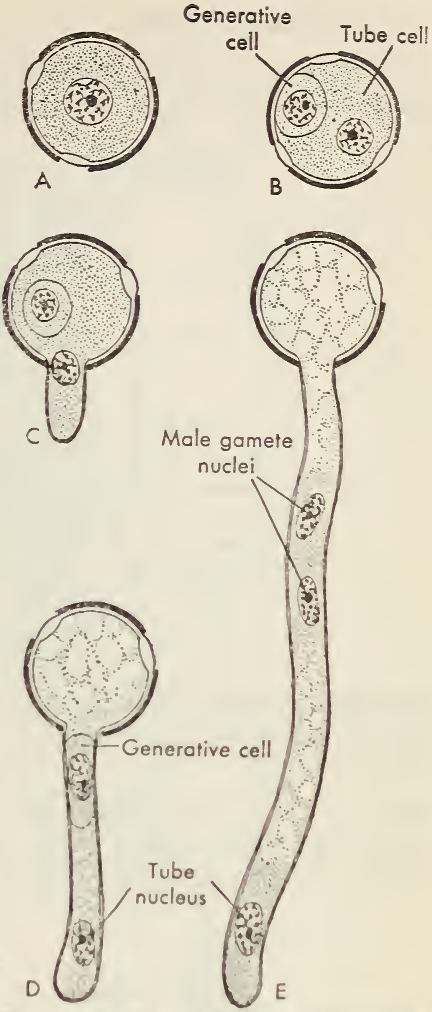


Fig. 14:9 The male gametophyte of a flowering plant. A microspore and its development into a male gametophyte. A, microspore; B, after the division which forms a generative and a tube cell, the male gametophyte is now a mature pollen grain; C, the pollen tube is beginning to form; D, migration of the generative cell into the pollen tube; E, after the division of the generative nucleus into two male gamete nuclei. All figures diagrammatic. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

E. POLLINATION

The transfer of pollen, called **pollination,** from the pollen sac to the stigma, whether it be the stigma of a flower in another plant or the same plant, is an essential link in the life cycle of a flowering plant. In most cases the pollen is either borne on the wind or carried on the bodies o insects. Wind-pollinated flowers are usually small and inconspicuous and have dry powdery pollen, whil flowers which are pollinated by insects are more conspicuous and ar often made attractive to their visitors by being highly colored and odoriferous and providing nectar. Th buttercup is pollinated by insects.

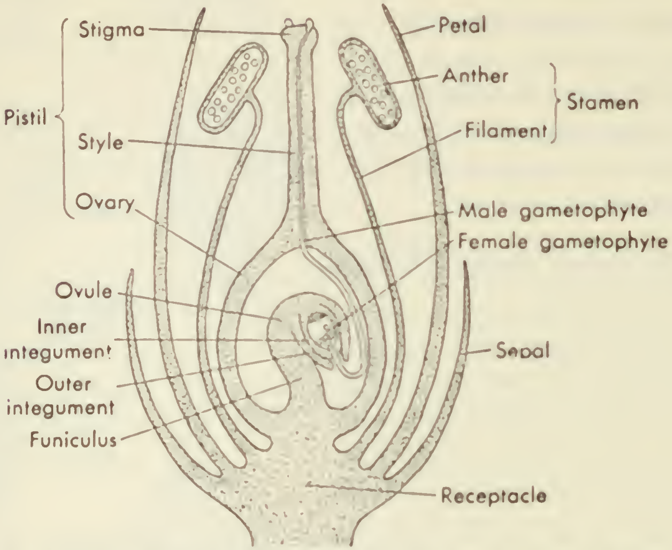


Fig. 14:10 Longitudinal section of a flower showing the growth of pollen tube from stigma to egg. Redrawn from Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

F. FERTILIZATION

When the pollen tube reaches th ovule it usually enters by way of th

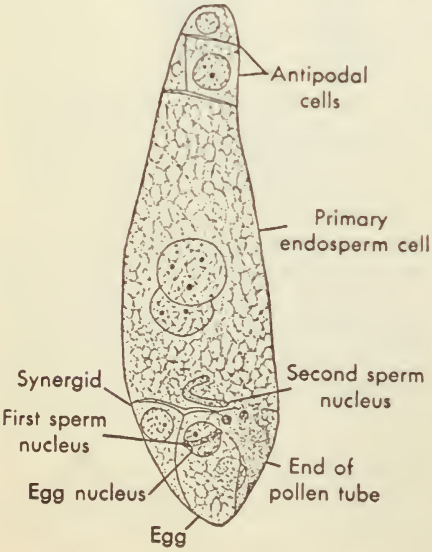


Fig. 14:11 Mature female gametophyte showing the union of one male nucleus with the egg nucleus, and the entrance of a second male nucleus into the primary endosperm cell. From Smith, Overton, *et al.*, *Textbook o General Botany*, The Macmillan Company.

micropyle and passes through the nucellus to the gametophyte (Fig. 14:10). On reaching the gametophyte the tip of the pollen tube bursts and the two sperm nuclei are discharged into it. One of the sperm nuclei fuses with the egg nucleus and a **zygote** is formed (Fig. 14:11). The other sperm nucleus moves into the primary endosperm cell and the three nuclei, namely, the two primary endosperm nuclei and the sperm nucleus, fuse to form a single **endosperm nucleus.**

G. THE SEED

The fertilization of the egg inaugurates changes which lead to the formation of the seed and fruit. We will consider first the zygote. The development begins with the division of the fertilized egg to form a short filament of cells. The cell of this filament farthest from the micropyle gives rise to the **embryo** proper while the rest of the filament forms a **suspensor** which forces the developing embryo toward the center of the endosperm (Fig. 14:12). Early in its development the embryo becomes differentiated into stem, root, and seed leaves or cotyledons.

It will be remembered that at the time of fertilization one of the sperm nuclei fused with the two nuclei of the primary endosperm cell to form a single primary endosperm nucleus. This primary endosperm nucleus divides repeatedly at first without cell division and the cytoplasm of the primary endosperm cell increases so that the young embryo is surrounded by a many-nucleated mass of protoplasm (Fig. 14:12). Later this mass divides into a many-celled structure called the **endosperm.** The fate of the endosperm differs in different species; in some it is digested and absorbed by the developing embryo; in others it forms

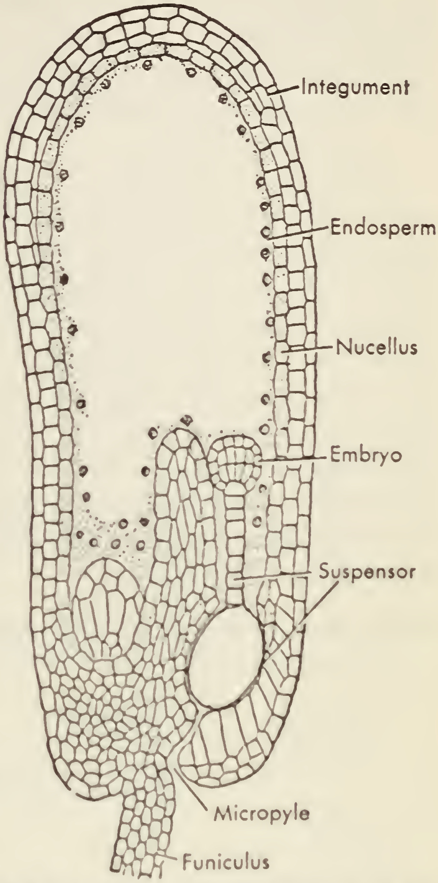


Fig. 14:12 Longitudinal section of an ovule of the shepherd's purse (*Capsella*), showing the early development of the embryo and the other structures which contribute to the formation of the seed. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

a part of the seed which is later absorbed by the young plant when it germinates.

During the development of the seed the antipodal cells and the synergids disappear as the female gametophyte becomes the endosperm. The nucellus also usually disappears.

The outer and inner integuments which, it will be remembered, are a part of the previous sporophyte generation form protective seed coats or a single seed coat.

In this description of the development of the seed we have accounted for the different parts of the ovule and have seen that three different generations in the life cycle of the plant have contributed. We may now consider the nuclear conditions in these different parts. The haploid number of chromosomes may be indicated by *n*, and the diploid number by 2*n*. The nuclei of the sporophyte will then have 2*n* chromosomes while the nuclei of the gametophyte and the gametes have *n*. The endosperm nuclei are, however, peculiar, since they have been shown to arise from the mitotic division of a nucleus which is formed from the union of two gametophyte nuclei and one sperm nucleus. Their chromosome number is 3*n*. The following table shows in tabular form the nuclear constitution of the parts of the seed:

TABLE 14:1. ORIGINS OF THE PARTS OF AN ANGIOSPERM SEED

SEED STRUCTURE	ORIGIN	GENERATION	NUCLEAR CONDITION
Seed coats	Integument	Sporophyte I	2*n*
Endosperm	Part of female gametophyte plus sperm nucleus		3*n*
Embryo	Zygote	Sporophyte II	2*n*

A seed is thus seen to be a ripened, i.e., fully developed ovule. The seed is an adaptation to life on land and the seasonal climatic changes to which life on land is particularly subjected. The embryo plant is protected during its early development and remains dormant until favorable conditions for its further development arise.

H. THE FRUIT

All these changes leading to the development of a seed take place in the ovule in the ovary, and while they are going on the ovary is changing into a fruit. The fruit of the buttercup is formed from a single carpel and contains only one seed. The carpel dries up, becomes closely applied to the seed and does not dehisce, i.e., break open, to liberate the seed. Such fruits are popularly taken for seeds; the botanical term for them is **akene**.

1. THE STRUCTURE AND GERMINATION OF THE SEED

The seed contains an embryo sporophyte and sufficient food materials stored, either in the seed leaves of the embryo, or in the endosperm, to provide for the growth of the embryo until it is able to manufacture its own food materials. Seeds differ much in general appearance and the proportions of the internal structures depending on where the food materials are stored and the stage of development of the embryo.

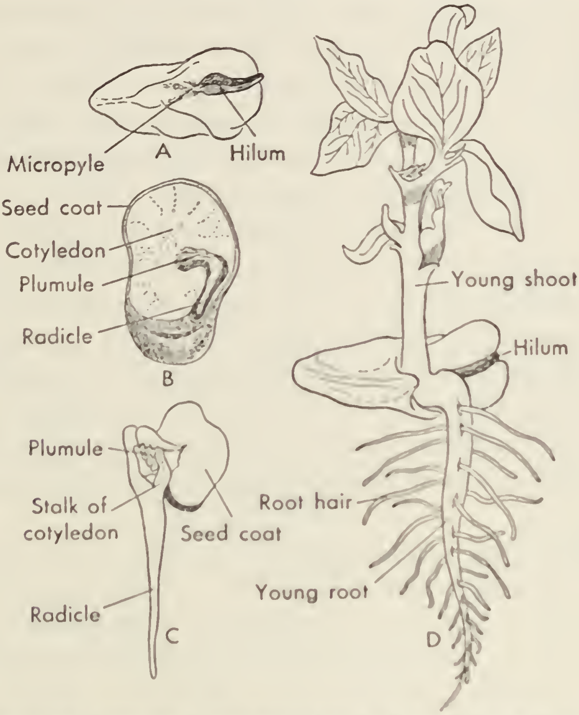


Fig. 14:13 Seed of the bean and its germination. A, seed on its side; B, longitudinal section of a bean seed; C, beginning of germination; D, young seedling. Redrawn after Francis Darwin, *Elements of Botany*, Cambridge University Press.

The structure of a **dicotyledon seed** without endosperm may be conveniently studied in the seed of the bean (Fig. 14:13). On the concave edge of the seed is a long narrow scar, called the **hilum.** This scar marks the surface where the stalk or **funiculus** of the ovule was attached. Just beyond the hilum on the same side of the seed is the persistent **micropyle.** When split longitudinally through the hilum, the seed is seen to be enclosed in two **seed coats** which are closely adherent to each other. The space inside the seed coats is almost entirely filled by the two seed leaves or **cotyledons** which, being mainly concerned with the storage of food materials, appear unlike ordinary leaves. Between the two cotyledons and the seed coats, on the side toward the hilum, is the remainder of the **embryo** (the cotyledons, being seed leaves, are part of the embryo). This part of the embryo consists of an embryonic shoot and root. The embryonic shoot is called the **plumule.** In the bean it consists of little more than two immature foliage leaves. In some seeds a short embryonic stem, called the **epicotyl,** extends above the cotyledons. Extending below the attachment of the cotyledons is the **hypocotyl** which ends in an embryo root called the **radicle.**

In the seed the development of the young sporophyte is suspended. That the embryo plant is still alive may be proved by showing that seeds respire, i.e., take in oxygen and give off carbon dioxide. Germination is the resumption of growth and development by the embryo sporophyte. For this, certain conditions are necessary. The most important of these are water, a favorable temperature, and oxygen. Water softens the seed coats, causes the seed to swell and burst the seed coats, facilitates the passage of oxygen into the seed and of carbon dioxide out of it, and by entering into the protoplasm facilitates the movement of food materials and the processes of metabolism. For most seeds there is an optimum temperature at which they develop most rapidly, a maximum temperature above which they will not develop, and a minimum temperature below which they will not develop. Oxygen is necessary for the process of respiration by means of which energy for the growth processes is liberated.

The germination of a bean seed will serve as an example of how the young plant establishes itself (Fig. 14:13, C, D). The radicle grows out near the micropyle and enters the ground. The hypocotyl then grows rapidly and lifts the cotyledons from the ground. The plumule grows upward and becomes a young shoot with leaves. During this time the food materials stored in the cotyledons are used by the growing root and hypocotyl. When freed from the seed coats, the cotyledons become green and carry on photosynthesis.

J. SUMMARY OF THE LIFE CYCLE OF A FLOWERING PLANT

The life cycle of a flowering plant (Fig. 14:14) may be compared with that of the pine or in more general terms with that of the fern. The "plant" which bears the flowers is the sporophyte. The flowers contain two kinds of sporophylls, stamens and carpels. The stamens are microsporophylls and the pollen sacs are microsporangia. The pollen grains formed in the pollen sacs are at first microspores. The carpels are megasporophylls and bear the ovules which are in large part megasporangia.

In the ovule are formed the megaspores of which only one is capable of development. This megaspore develops in the ovule into a female gametophyte called in this case the embryo sac. Throughout its life the female gametophyte is dependent on the sporophyte for the necessities of its existence and in its mature state in most flowering plants contains only eight nuclei, one of which is contained in the egg cell. The male gametophyte begins its development while still in the pollen sac, the protoplasm in the pollen grain dividing into a tube cell and a generative cell. Further development of the male gametophyte is conditional on the pollen being transferred to a stigma. Here the pollen tube grows down to the egg cell and the generative nucleus divides, giving rise to two sperm nuclei. One of the sperm nuclei enters the egg cell and fertilization leads to the development of an embryo and the beginning of a second sporophyte generation. The other sperm nucleus unites with the two nuclei of the primary endosperm and the division of the resulting nucleus leads to the formation of the endosperm. Three different kinds of cells take part in the formation of the seed and are represented by the embryo, the endosperm, and the seed coats. The nuclei of all the gametophyte stages are haploid (n), those of the sporophyte stages are diploid ($2n$). The endosperm nuclei usually have the chromosome number $3n$.

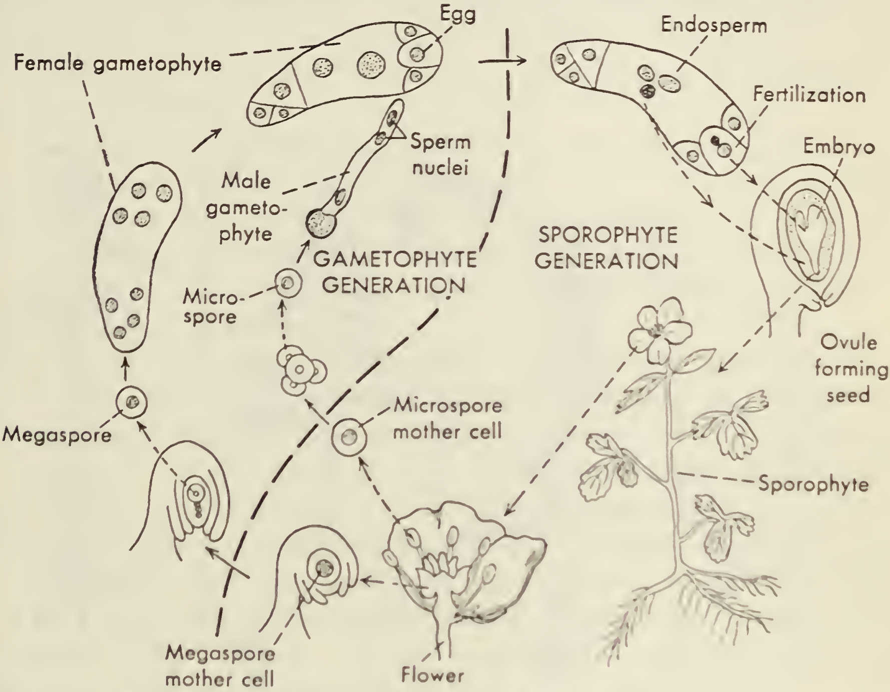


Fig. 14:14 Diagram of the life cycle of a flowering plant.

2. THE ALTERNATION OF GENERATIONS AND THE EVOLUTION OF THE SPOROPHYTE

In considering the evolution of the plant body in the Bryophyta, Pteridophyta, and Spermatophyta we must not forget that in plants where there is an alternation of generations, we can properly compare only plant bodies which belong to the same generation (Fig. 14:15).

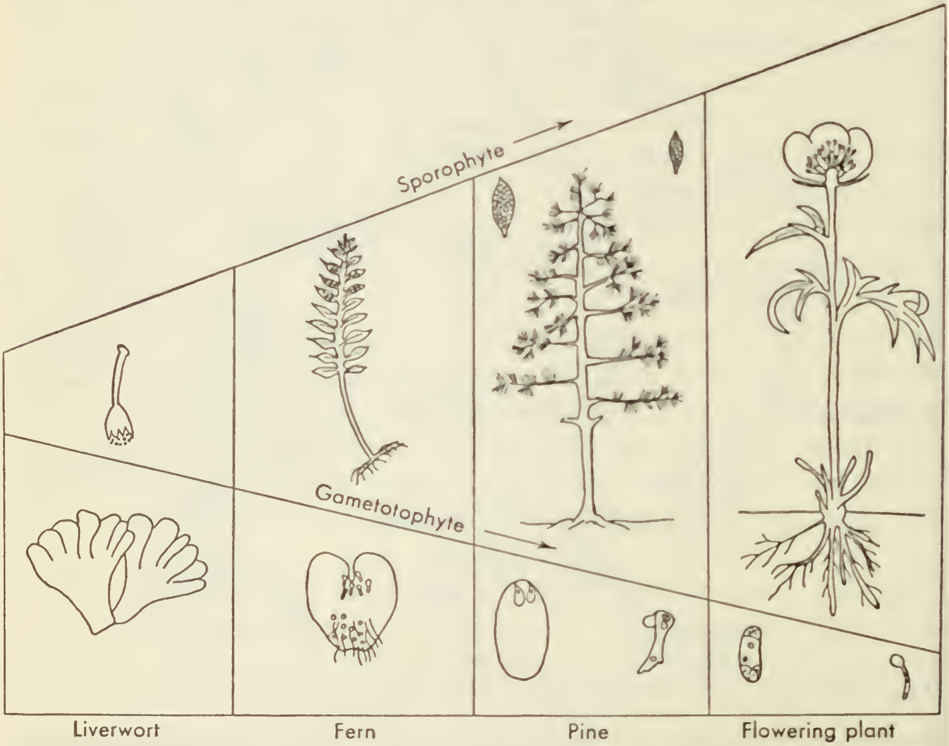


Fig. 14:15 The relative development of the sporophyte and gametophyte generations in the evolution of a flowering plant from the liverwort stage.

Thus in comparing a moss with a flowering plant we are tempted to be influenced by the superficial resemblance of the gametophyte of the moss with the sporophyte of a flowering plant, yet the sporophyte of the flowering plant cannot be descended from the gametophyte of a moss since they belong to different generations and are fundamentally different, for example in nuclear constitution, the one having haploid nuclei and the other having diploid nuclei. The similarity of the plant bodies of the moss gametophyte and the sporophyte of some flowering plants is an example of **parallel evolution** also called **convergence.** By convergence is meant a similarity between organisms which is not due to closeness of relationship by descent.

In attempting to trace the evolution of the sporophyte we may begin with the sporophyte of a liverwort such as *Marchantia* which consists of little more than a cup enclosing spores and which is entirely dependent for its nourishment on the gametophyte. The sporophyte of a moss such as *Funaria*, although probably not on the direct line of descent of the higher plants, shows us some of the steps which may have occurred: namely the development of a stalk bearing the spores in a capsule or sporangium, and the development of specialized sporophyte tissues including cells containing chloroplasts and capable of carrying on photosynthesis.

Passing to the Pteridophyta we find that in the fern the sporophyte is an independent plant possessing a stem, leaves, and roots. With the appearance of these structures is associated the development of conducting and supporting tissues. The sporophyte of the Spermatophyta shows a still greater complexity than that of the Pteridophyta, especially in its conducting tissues.

In many Pteridophyta the spores are borne on special leaves or sporophylls and in certain forms two kinds of spores, microspores and megaspores, are present, giving rise respectively to male and female gametophytes. In the Spermatophyta the male and female gametophytes are minute dependent plants, the female gametophyte undergoing its entire development within the ovule, where fertilization and the early development of the young sporophyte occur, leading to the formation of the seed. The many and complex varieties of flowers have been evolved as adaptations of different methods of pollination especially by insects; the equally numerous and complex varieties of seeds and fruits have developed as adaptations to the dispersal of the species.

The almost continuous series of stages from the mere ball of spore mother cells to the complex structure of a hardwood tree provide strong if not convincing evidence of the evolution of land plants from some simple, probably algal, ancestor or ancestors. This evolution of the sporophyte has been accompanied by a corresponding retrogression of the gametophyte generation, necessitated no doubt by the exigencies of life on land (Fig. 14:15).

3. TYPES OF INFLORESCENCES, FLOWERS, SEEDS, AND FRUITS

A. *INFLORESCENCES*

The flowers of the buttercup occur singly and each is borne on the end of a flower stalk or **peduncle** which arises from the axil of a foliage leaf. In many plants the flowers are arranged in groups on the end or on branches of the peduncle forming an inflorescence. Inflorescences are classified according to their method of growth into racemose and cymose inflorescences. In a **racemose inflorescence** the youngest flowers are nearest the tip of the main stalk or peduncle or on the youngest branches which are those nearest the tip. In a **cymose inflorescence** the reverse is the case and the oldest flowers are at the tip of the main axis and on the branches nearest to it. Either kind of inflorescence may be either simple or compound according to the method of branching. A simple inflorescence is one in which the flowers are either sessile, i.e., without separate stalks, or on branches which do not again branch. In a compound inflorescence the branches give rise to branches which may again branch.

Simple racemose inflorescences include the spike, raceme, corymb, umbel, and head (Fig. 14:16). In a **spike** the main axis is elongated and the flowers are sessile or practically so. A familiar example is the plantain (genus *Plantago*). When the axis of a spike is fleshy or thickened the inflorescence is called a **spadix.** Usually it is enveloped in a large and peculiar leaf called a **spathe** as in the common jack-in-the-pulpit (genus *Arisaema*) (Fig. 39:6). The short, hanging, scaly spikes of many common trees, e.g., willow (genus *Salix*) are called **catkins.** A **raceme** is similar to a spike but the flowers are on stalks or pedicles. The lily of the valley (genus *Convallaria*) and the common red currant (genus *Ribes*) are examples. In a **corymb** the pedicles of the older flowers are longer than those of the younger so that the flowers come to be in one plane. An example is the hawthorn (genus *Crataegus*). In an **umbel** the main axis is short and the pedicles are of approximately equal length so that the flowers come to be on a portion of a sphere and form a "ball." The flowers of the cherry form a simple umbel. In a **head** the axis is short and the flowers are arranged in a globular mass as in the clover (genus *Trifolium*) or on a disc forming what the older botanists called a **com-**

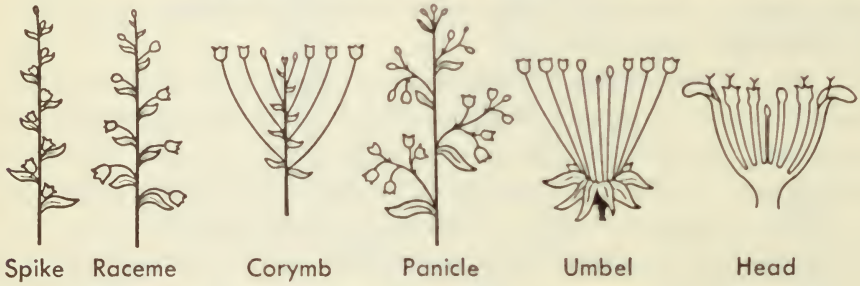


Fig. 14:16 Diagrams to show types of racemose inflorescences.

pound flower, a structure which is characteristic of the family Compositae. An example is the sunflower (genus *Helianthus*).

A compound spike is seen in wheat (genus *Triticum*), (Fig. 17:1) a compound raceme, called a **panicle,** is seen in the oat (genus *Avena*), a compound umbel in the parsnip (genus *Pastinaca* and many members of the order Umbellales).

Cymose inflorescences are much less common than racemose. The peduncle is usually branched giving rise to what is called a **cyme.** A simple cyme is seen in the crab apple (genus *Pyrus*), a compound cyme in the hydrangea (genus *Hydrangea*).

B. TYPES OF FLOWERS

Flowers show great variety of structure and their characteristics are much used in the classification and separation of the different genera and species of flowering plants. Many of the features may be conveniently shown in a **floral diagram** (Fig. 14:17).

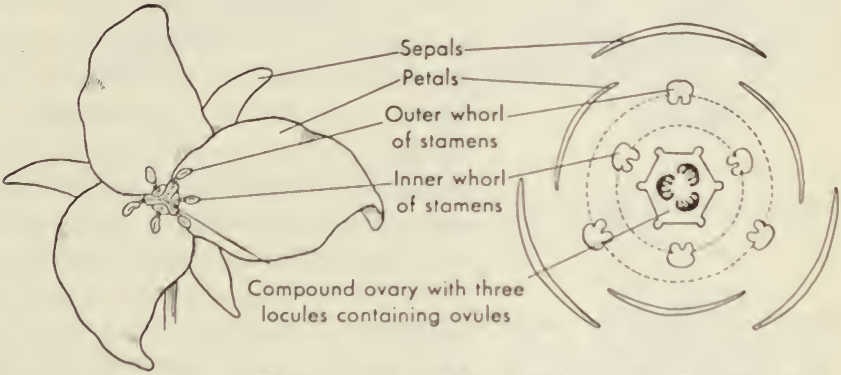
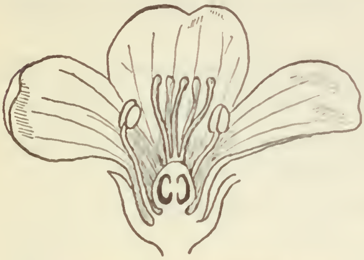


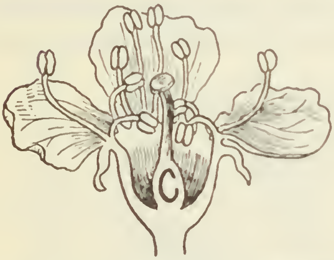
Fig. 14:17 The flower of *Trillium* (subclass Monocotyledoneae). On the left, a view looking into the flower. On the right, a floral diagram. Redrawn from Chamberlain, *Elements of Plant Science*, by permission of McGraw-Hill Book Company, Inc.

The **symmetry** of the flower as a whole is usually radial. In this case the flower is said to be **regular** as in Fig. 14:17. Many flowers are bilaterally symmetrical and are then said by botanists to be **irregular** (Fig. 14:19). Typically a flower has the same number of sepals and petals but there are often two whorls of stamens, i.e., twice as many stamens as petals; thus, the flower in Fig. 14:17 has three sepals, three petals, six stamens, and three carpels. Such a flower is said to be **numerically symmetrical.** Flowers are termed **monomerous, dimerous, trimerous, tetramerous, pentamerous,** and **hexamerous** according as there are one, two, three, four, five, or six members in a whorl. Most flowers are either pentamerous, trimerous, or tetramerous in the order named.

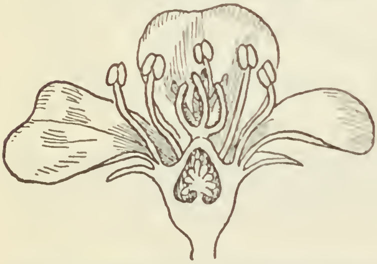
The number of members in any one or more of the whorls may deviate from that of the rest. This most frequently happens in the case of the stamens and carpels. The number of stamens is commonly **multiplied** so that there are two or more whorls, indeed two whorls occur more often than one. The stamens may be reduced in number, a condition which occurs in orchids. The number of carpels is frequently reduced. Thus there may be only three or one in a pentamerous flower.



A. Hypogynous Flower (superior ovary)



B. Perigynous Flower (half inferior ovary)



C. Epigynous Flower (inferior ovary)

Fig. 14:18 Types of flowers. Redrawn after Asa Gray, *Structural Botany*, The Mamillan Company.

Suppression or **abortion** occurs when an entire whorl is absent from a flower. This is most conspicuous when either the stamens, which collectively compose the **androecium,** or the pistil or pistils which compose the **gynoecium,** are wanting. Such a condition gives rise to **unisexual** or **imperfect** flowers. Flowers with stamens but without pistils are said to be **staminate** or **male.** Flowers with pistils but without stamens are said to be **pistillate** or **female.** When the male and female flowers occur on the same plant the species is **monoecious.** When they occur only on different plants the species is **dioecious.**

The parts of a plant may grow together and become united in various ways. When the members of the same whorl adhere the condition is called **coalescence.** This is most frequent in the case of the gynoecium and leads to the formation of a compound pistil. When the petals are united the flower is said to be **sympetalous.** Another kind of union, called **adnation,** occurs when members of different whorls unite. The union of the stamens for a portion of their length with the petals is the commonest kind of adnation.

As already referred to, the carpels are frequently united to form a compound pistil. In a **compound pistil** the usual arrangement is for each carpel to surround a locule and for the portions of the carpels which correspond to the margins of the sporophylls to meet in the axis of the ovary. The number of locules is then equal to the number of carpels. The ovules are then attached at the axis which is called **axial placentation** (Fig. 14:18 A). Sometimes the partitions between the locules disappear giving rise to **free central placentation** (Fig. 14:18 C). In another arrangement the margins of the carpels join in the outer wall of the ovary to form a single large locule (Fig. 14:18 B). The ovules are then attached near the lines of fusion, and the placentation is called **parietal.**

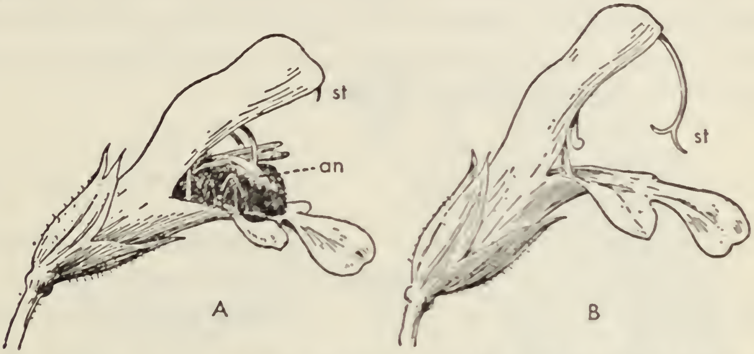


Fig. 14:19 Pollination in the common sage, *Salvia*. A, a bee is visiting a flower and receiving pollen from two anthers, *an*, which turn down upon its body as the bee enters. B, a flower with the anthers in the erect position and the stigma, *st*, ready to receive pollen. After Lubbock, from Bergen and Davis, *Principles of Botany*, Ginn and Company.

When the receptacle is rounded or club-shaped and the parts of the flower arise directly from it as is the case in the lily (genus *Lilium*) the flower is said to be **hypogynous** (meaning beneath the gynoecium), and the ovary is said to be a **superior ovary** (Fig. 14:18 A). When the receptacle grows up around the ovary but remains separate from it forming a cup or tube to the upper margin of which the other parts of the flower are attached the flower is said to be **perigynous** (meaning around the gynoecium) (Fig. 14:18 B). When the receptacle grows about and completely encloses the ovary adhering to it and the other parts arise on top of it the flower is said to be **epigynous** (meaning on the gynoecium) and the ovary is called an **inferior ovary** (Fig. 14:18 C).

Many flowers are **self-pollinated,** i.e., pollen from the stamens passes to the stigma of the same flower or to the stigma of another flower on the same plant. **Cross-pollination** occurs when pollen from one plant is transferred to the stigma of a flower on another plant. The two chief methods of transfer of pollen are by wind and by insects. Both of these methods usually lead to cross-pollination. Pollination by wind requires the production of large quantities of pollen and is somewhat uncertain. Wind-pollinated flowers are usually small and inconspicuous. Insect pollination has the advantage of requiring less pollen. In many cases special adaptations have been developed to attract insects and secure the transfer of pollen by them. An interesting example is found in the common sage. In the flower of this plant the anthers mature earlier than the stigmas. By a peculiar mechanism (Fig. 14:19) the two anthers when ripe with pollen are pressed down on the body of the visiting insect while the still immature stigma is protected in the upper part of the flower. As the flower becomes older the anthers wither and the style elongates and bends downward, placing the stigma in the path of the visitor. Even more complicated mechanisms to ensure cross-pollination by insects are found in the orchids (family Orchidaceae).

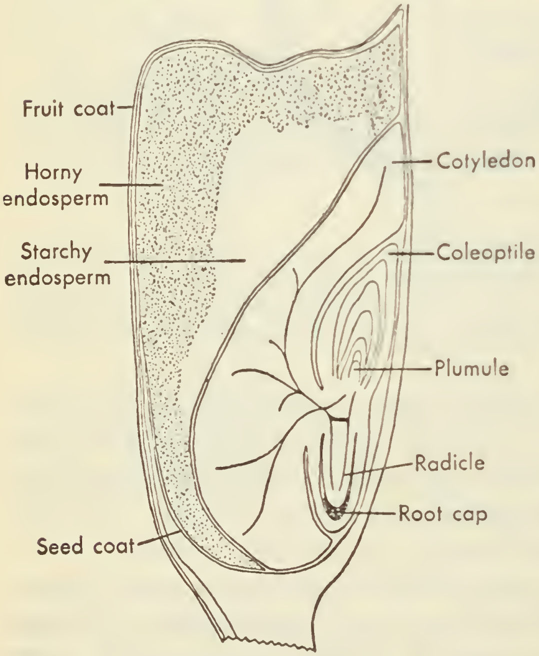


Fig. 14:20 Longitudinal section of a grain of corn. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

C. TYPES OF SEEDS

Seeds may be divided into those which contain an endosperm and those which do not. In the case of seeds without an endosperm, an endosperm may be formed in the early stages and be absorbed into the embryo. Seeds may also be classified according to the number of cotyledons present into monocotyledonous, dicotyledonous, and polycotyledonous.

The bean seed (Fig. 14:13) described in the account of the life cycle of a flowering plant is an example of a **dicotyledonous seed** without endosperm. The seed of the corn, *Zea mays* (Fig. 14:20) is an example of a **monocotyledonous** seed with an endosperm, the seed of the pine (Fig. 13:9) is an example of a **polycotyledonous** seed with endosperm. The seeds of most monocotyledons and gymnosperms have an endosperm. Some dicotyledons have an endosperm and some do not.

A considerable portion of the corn seed is occupied by the endosperm which consists of horny and starchy portions. To one side of the endosperm is the single cotyledon, and between it and the seed coats is the remainder of the embryo. There is an epicotyl and two or more immature foliage leaves, covered with a caplike structure called the **coleoptile.**

D. TYPES OF FRUITS

A **true fruit** is developed from an ovary and its contained seed or seeds. However, many common fruits involve other structures such as the receptacle, petals, and sepals. Such fruits are called **accessory fruits.** The tomato, *Lycopersicum*, is developed from a single superior ovary and is a true fruit. The gooseberry, *Ribes*, on the other hand is developed from an inferior ovary and the receptacle takes part in its formation. It is therefore an accessory fruit.

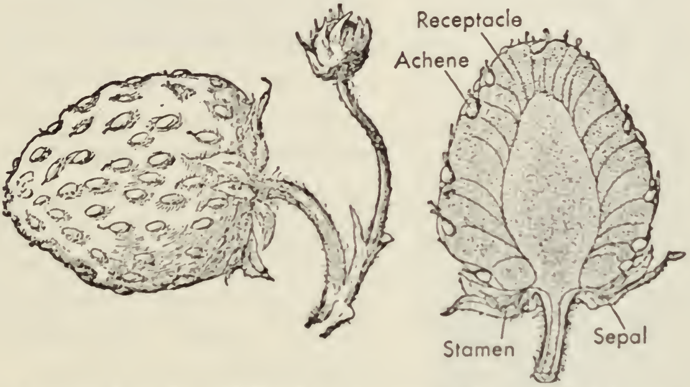


Fig. 14:21 A strawberry, an aggregate fruit, drawn in surface view and in longitudinal section. The "seeds" or "achenes" are formed from single ovaries. The fleshy part is the receptacle of the flower. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

Another grouping of fruits is into simple, aggregate, and multiple. A **simple fruit** contains a single ripened ovary, which, however, may be a compound ovary. The tomato and gooseberry, referred to above, are simple fruits. An **aggregate fruit** is developed from a single flower and contains several ripened ovaries. The strawberry is an example of an aggregate fruit (Fig. 14:21). It is also an accessory fruit, the fleshy portion being developed from the receptacle of the flower. The ovaries form the small hard bodies distributed on the surface of the strawberry. A **multiple fruit** is developed from a cluster of flowers or an inflorescence which has the form of a short spike. The pineapple is an example (Fig. 14:22).

Simple fruits may be divided into fleshy and dry. In a **fleshy fruit** the ovary, and accessory parts if present, develop into the fleshy or succulent part. In a **dry fruit** this portion becomes dry and hard. Common types of simple fleshy fruits are the drupe, berry, and pome.

The **drupe** is seen in such fruits as the plum, peach, cherry, apricot, and almond. In this type of fruit the outermost layers of the ovary wall form the skin, the intermediate layers form the fleshy portion, while the innermost layers form the hard "stone" inside which is the comparatively soft seed (Fig. 14:23). In the almond the intermediate layers are fleshy in the earlier stages and later become fibrous. In this case the portion eaten as the "nut" is really the seed.

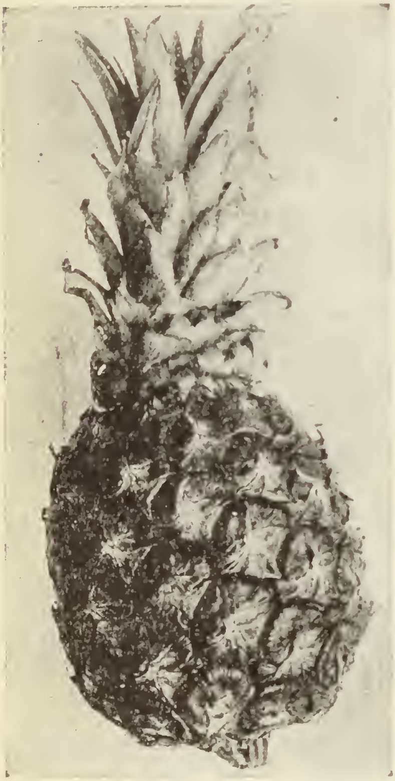


Fig. 14:22 A pineapple, a multiple accessory fruit. From Smith, Gilbert *et al.*, *Textbook of General Botany*, The Macmillan Company.

A **berry** may be developed from a single or a compound ovary. The inner portion of the ovary wall and the partitions between the locules are thick and juicy. A berry is easily distinguished from a drupe as it has no inner "stone," and the seeds appear to be imbedded in the juicy mass. The fruit of grape, tomato, orange, watermelon, squash, and cucumber are berries.

The **pome**, from the French for "apple," is somewhat similar to a berry but the greater part of the fleshy tissue is developed from a floral tube which consists of the bases of the sepals, petals, and stamens, and the inner portion which forms the "core" is papery and developed from the ovary (Fig. 14:24). The outer ends of the sepals often persist at the end of the apple opposite to that attached to the stalk. Examples include apple, pear, and quince.

Simple **dry fruits** are distinguished as dehiscent and indehiscent. **Dehiscent** fruits split open when they are ripe. Two common forms of dehiscent fruits are the legume and the capsule. A **legume** such as the pea or bean is formed from a single carpel and splits open along two sutures, one corresponding to the midrib of the carpel, the other to the line along which the right and left margins are fused (Fig. 14:25). The peanut, although it does not spontaneously split open is, nevertheless, classified as a legume. A **capsule** is formed from two or more carpels and may dehisce in different ways depending on the species. The capsule of the poppy, for example, opens by a number of pores, while that of the lily splits along the midribs of the carpels.

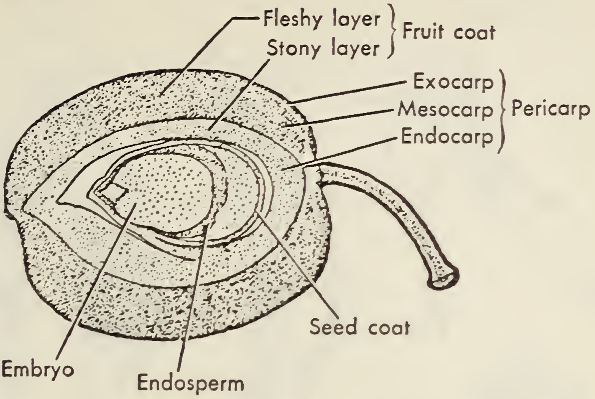


Fig. 14:23 A plum, an example of a drupe, shown in longitudinal section. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

Common forms of simple, dry, **indehiscent fruits** are the achene, grain, samara, and nut. An **achene** is a one-seeded fruit with the seed attached to the ovary at one point only. Examples are found in the buttercup, sunflower, and buckwheat. A **grain** is a one-seeded fruit with the seed attached everywhere to the ovary (Fig. 14:20). Grains include corn and wheat, rice, barley, and the other plants of the grass group. In a **samara,** which may be a one- or two-seeded fruit, the wall of the ovary forms winglike outgrowths. The fruit of the maple, ash, and elm are samaras. A **nut** may develop from an ovary containing one or

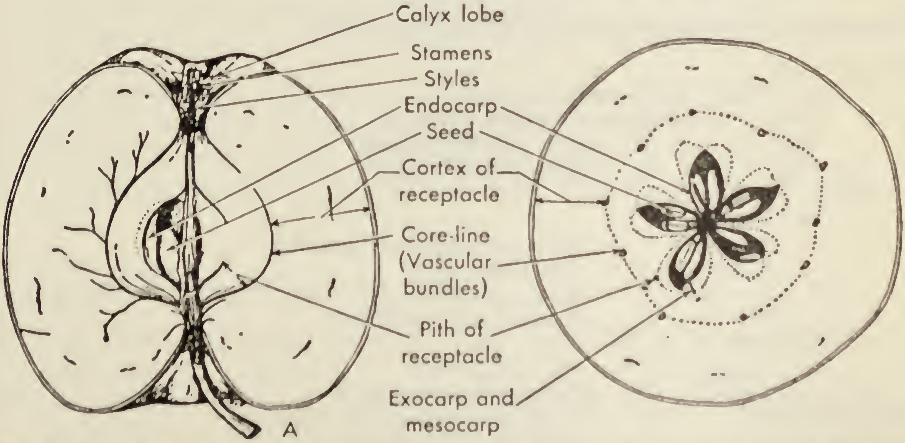


Fig. 14:24 An apple, an example of a pome, in section showing the structure of the fruit. Reproduced by permission from Holman and Robbins, *Textbook of General Botany*, John Wiley & Sons, Inc.

more ovules, but usually only one ovule develops into a seed. The hard outer shell is formed from the inner portion of the ovary wall, the outer portion forming the "husk." The almond, horse chestnut, and Brazil nut are seeds, not fruits.

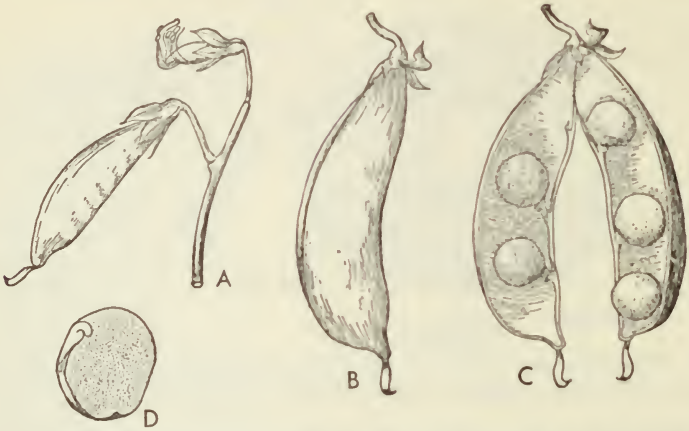


Fig. 14:25 Fruit and embryo of the pea, an example of a legume. A, flower and young fruit; B, mature fruit; C, mature fruit split open; D, embryo with one cotyledon removed. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

TABLE 14:2. CLASSIFICATION OF FRUITS

(Some of these fruits are not true fruits but accessory fruits.)

Simple Fruits					
	Fleshy (all fleshy fruits are indehiscent)				
		Drupe		Examples:	plum, peach, cherry
		Berry		"	grape, tomato, orange
		Pome		"	apple, pear, quince
	Dry				
		Indehiscent			
			Achene	"	buttercup, sunflower, buckwheat
			Grain	"	corn, wheat, grass
			Samara	"	maple, ash, elm
			Nut	"	chestnut, acorn, hazelnut
		Dehiscent			
			Legume	"	pea, bean, peanut
			Capsule	"	lily, poppy, Jimson weed
Aggregate Fruits				"	strawberry, raspberry, blackberry
Multiple Fruits				"	mulberry, pineapple, fig

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Questions

1. Explain how "A flower is best regarded as a series of whorls of leaves."
2. Compare the central portion of a buttercup, the part containing the carpels, with the carpellate cone of a pine.
3. Make a floral diagram of a common flower, naming the parts.
4. Explain what is meant by hypogynous, perigynous, and epigynous flowers and superior, half inferior, and inferior ovaries.
5. Describe the pollination of the common sage.
6. Compare the male and female gametophytes of a flowering plant with those of a pine.
7. Describe the development of the seed.
8. State the conditions necessary for the germination of a seed.
9. Compare the life cycle of a flowering plant with that of the pine.
10. In what respects is a flowering plant better adapted to life on land than a fern?

Suggestions for Further Reading

Pool, Raymond J., *Flowers and Flowering Plants*, McGraw-Hill Book Company, Inc., New York, 1929.

Holman, Richard M., and Wilfred W. Robbins, *A Textbook of General Botany*, John Wiley & Sons, Inc., New York, 1934.

CHAPTER 15

The Root, Stem, and Leaf of the Seed Plants

This chapter will be devoted to a study of the vegetative organs of the flowering plants. These are the root, stem, and leaf. They are chiefly concerned with securing and storing food. We begin with the root because its development can be easily followed in a seedling.

1. THE ROOT

The main functions of the root are absorption of water and inorganic salts from the soil and anchorage in the ground for support of the shoot. In many plants the roots make up a system quite as extensive as that of the stem and leaves above ground and they play almost as important a role.

A. THE ROOT TIP

(1) GENERAL FEATURES AND DEVELOPMENT

The most important parts of the root for the plant are the tips of the finest branches, because it is here and here only that the root absorbs water from the soil. We shall, therefore, begin our study of the root with the tip of the root of a young seedling. The advantage of the root of the seedling for a preliminary study lies in the fact that it can be grown in water alone and obtained for microscopic study free from the dirt which adheres to a root grown in the soil.

If the root of such a seedling be examined under the microscope it will be found that the surface is covered, from a point somewhat behind the extreme tip, for a considerable distance with fine transparent hairs (Fig. 15:1). These are the **root hairs.** Further study of a root hair reveals that it is a process extending from one of the epidermal cells which form the outer layer or **epidermis** of the root (Fig. 15:2). There are no cross walls in the root hairs. Each root hair is merely a part of an epidermal cell. The nucleus of the cell is usually to be found in the root hair. The root-hair cell contains a large vacuole.

The root tip can be divided into a number of regions which are not sharply separated and overlap to a considerable extent. The extreme tip is covered and protected by the **rootcap,** the outer cells of which are continually wearing away (Fig. 15:1) as the root pushes its way through the soil. Just above the rootcap the cells are small, cubical, filled with protoplasm, and frequently in the process of division. This region of the root is called the **embryonic region** because it is here that there is the most active production of new cells. As we pass along the root from the embryonic region we come into regions in which the cells are progressively more and more differentiated. Cells become differentiated as they become specialized. The term **differentiation** applies to the structural changes which accompany specialization. Differentiation leads to the formation of tissues. A **tissue** is a group of cells which are similar in structure and perform similar functions.

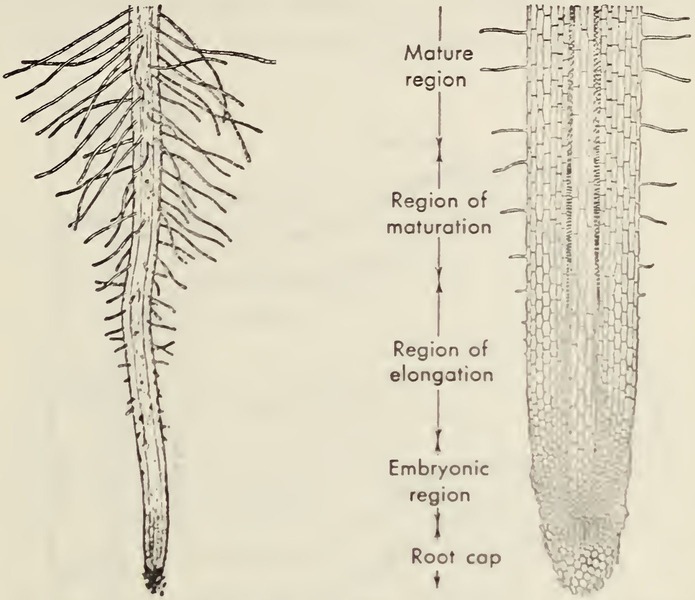

Fig. 15:1 Structure of a root tip. On the left, a root tip of a grass seedling grown in water. From Haupt, *Fundamentals Biology*, by permission of the McGraw-Hill Book Company. On the right a diagram of a longitudinal section of a root tip. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

In a root tip the process of differentiation can be easily followed. In order to see the various stages through which a group of cells pass to become a specialized tissue it is only necessary to pass the eye along the root, the least differentiated or morphologically youngest cells being nearest the root tip. Four regions can be distinguished. First is the embryonic region already considered. Next comes a **region of cell elongation** in which the cells are growing in length. The third region is the **region of cell differentiation.** Here the cells begin to undergo specialization and differentiation. The cells of the epidermis form root hairs. The cells of the axial portion begin to differentiate into conducting tissues.

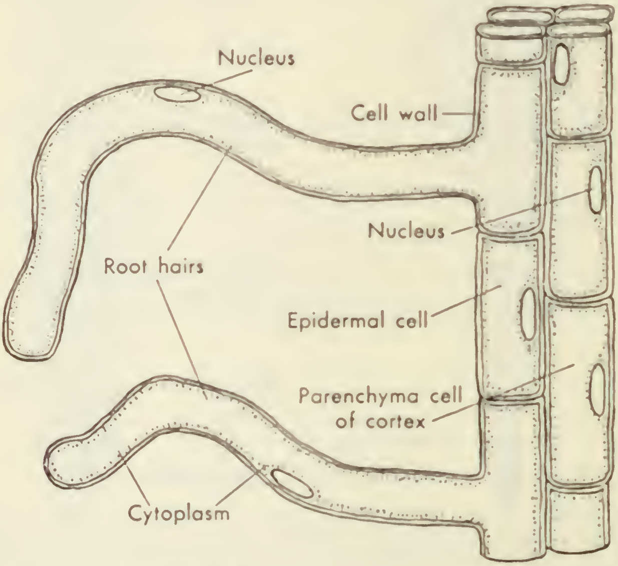

Fig. 15:2 Root hairs.

The fourth and last region is called the **mature region.** It includes the rest of the root. Here the cells have become differentiated into the various tissues of the adult root.

(2) PRIMARY TISSUES

Cell differentiation leads to the formation of tissues in the mature region of the root. In the mature region of the root tip of a young root these tissues are called **primary tissues** because they are formed directly by elongation and differentiation from the cells of the embryonic region of the root. The tissues of the root are best studied in thin sections. We will first consider a cross section, taken at right angles to the axis of the root in the region of root hairs which includes the youngest part of the mature region (Fig. 15:3). In such a region the outer layer of cells which was in contact with the soil is the **epidermis.** The epidermal cells are somewhat flattened parallel to the surface of the root and elongated in the direction of the axis. The term epidermis is generally applied to a tissue composed of cells covering a surface. In the case of the root many of the epidermal cells, in addition to covering the surface, develop root hairs. Within the epidermis is the **cortex,** the inner boundary of which is formed by a layer of cells, the **endodermis,** somewhat similar in cellu-

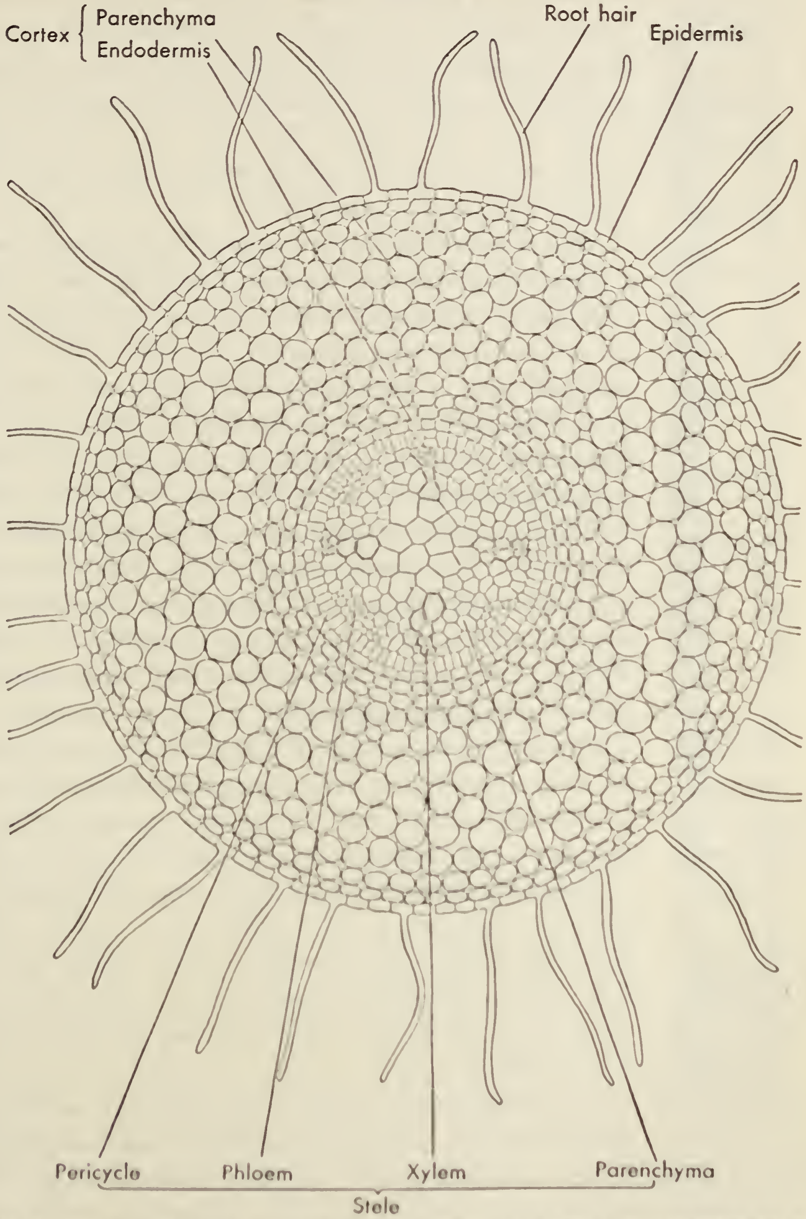

Fig. 15:3 Cross section of a root of a sunflower plant at a level at which cambial activity has not yet begun and showing only primary tissues. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

lar structure to the epidermis. The cells of the cortex, which occupy the space between the epidermis and the endodermis, form a type of tissue called **parenchyma.** Parenchyma cells are not elongated and usually measure about the same in all directions. They are thin walled and may be somewhat irregular in shape. Their protoplasts contain large vacuoles which serve for the storage of water and food materials. Parenchyma cells occur not only in the root but in many different parts of the plant. In them is stored the starch and sugar of fleshy roots such as the carrot and beet.

The tissues inside the cortex make up the **stele.** Surrounding the stele and forming its outer layer, just inside the endodermis, is the **pericycle,** composed of one or more layers of cubical cells. Within the pericycle is a conspicuous star-shaped group of cells. This appearance is the result of cutting across strands of primary **xylem,** or woody tissue, which run lengthwise in the stele. The first cells to be differentiated in these strands are called **tracheids** (Fig. 15:4). These are elongated cells with pointed ends and walls thickened in certain places. In some tracheids the cell wall is thickened along a spiral, the part of the wall between the coils of the spiral remaining thin; these are **spiral tracheids.** In other tracheids the thickening of the cell wall takes the form of a series of rings, giving rise to **annular tracheids.** Further thickening of the wall may occur, leaving only pits where the cell wall is thin. The tracheid is then called a **pitted tracheid.** Tracheids are formed while elongation of the root is still taking place. After a time the protoplasts of the tracheids die, leaving the hollow cells to conduct water through the root. The protoplasts of the cells of the other primary tissues remain alive.

As development in the root proceeds, additional cells along the inner edges of the strands of primary xylem also develop into primary xylem. Many of the cells which differentiate into xylem after the forma-

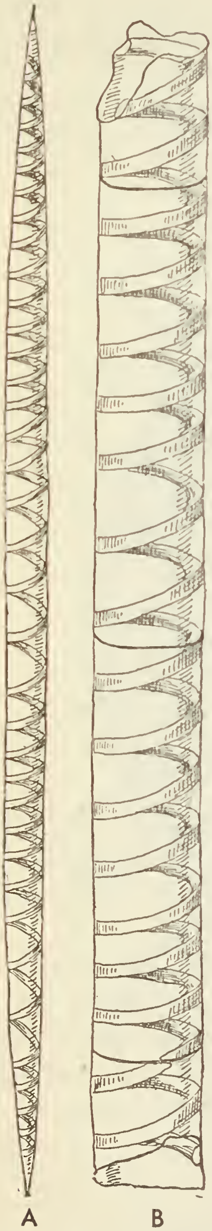

Fig. 15:4 A, a tracheid with spirally thickened wall; B, a portion of a vessel with spirally thickened wall. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

tion of the tracheids form vessels. A **vessel** is formed when a number of elongated cells join end to end (Fig. 15:4 B). The side walls develop thickenings similar to the tracheids. Thus there are **spiral vessels, annular vessels,** and **pitted vessels.** The end walls where the cells forming a vessel join are dissolved away and disappear. As in the case of tracheids, the protoplasts of the cells forming vessels die, leaving only the cell walls in the form of hollow tubes.

In the cross section of the mature region of the young root between the strands of primary xylem, and alternating with them, are to be seen sections of the strands of **primary phloem.** These are composed of sieve tubes, companion cells, and parenchyma (Fig. 15:5). A **sieve tube** is formed by the union end to end of a number of elongated cells, in a way similar to that in which a xylem vessel is formed, excepting that the side walls are not thickened to the same extent and the end walls separating the cells persist. In these end walls pores are developed through which the cytoplasm of the cells becomes continuous. Along the sieve tubes of most plants lie **companion cells,** the lengths of which are either equal to or shorter than the portion of a sieve tube which arises from one cell. The protoplasts of the companion cells persist and retain their nuclei. The nuclei of the cells which form the sieve tubes disappear. The protoplasm forms a strand extending through the sieve tube and fanning out at the ends. Through the pores pass fine strands of protoplasm connecting the protoplasm in adjoining tubes.

In the xylem vessels and tracheids, water, dissolved salts, and other materials are conducted from the tips of the roots to the leaves. The sieve tubes and the companion cells conduct organic food materials manufactured in the leaves and other chlorophyll-bearing parts of the plant. Tracheids, vessels, and sieve tubes are all types of **conducting** or **vascular tissue.**

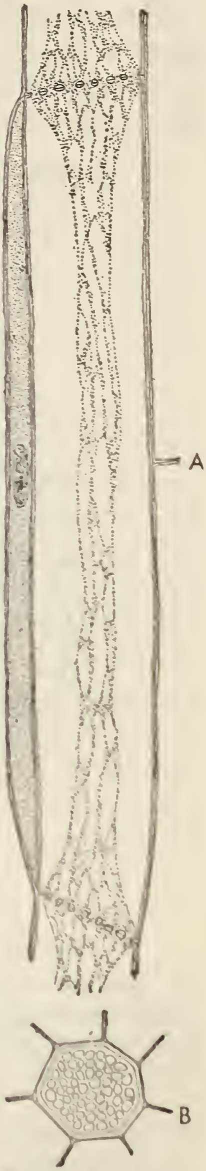

Fig. 15:5 A sieve tube. A, a longitudinal section of a segment (part formed from one cell) of a sieve tube and its companion cell which appears with its nucleus on the left, from the secondary phloem of a root of the squash; B, a view of an end wall of a tube. From Smith, Overton, *et al., Textbook of General Botany.* The Macmillan Company.

B. THE MATURE ROOT—SECONDARY TISSUES

The tissues described in the previous section, including the primary xylem and the primary phloem, are all developed by the differentiation of cells arising directly by cell division from the embryonic region. For this reason they were called **primary tissues.** In the mature region of the roots and stems of dicotyledons certain cells remain undifferentiated and retain their embryonic character, forming a tissue which is called **meristem.** In the root (and also in the stem) the chief meristem, known as the **cambium,** lies between the xylem and phloem, bounded by the phloem on the outside and xylem on the inside. It is composed of small cubical cells which during the growing season divide frequently. Growth in thickness of the root above the root tip is due to tissues which arise

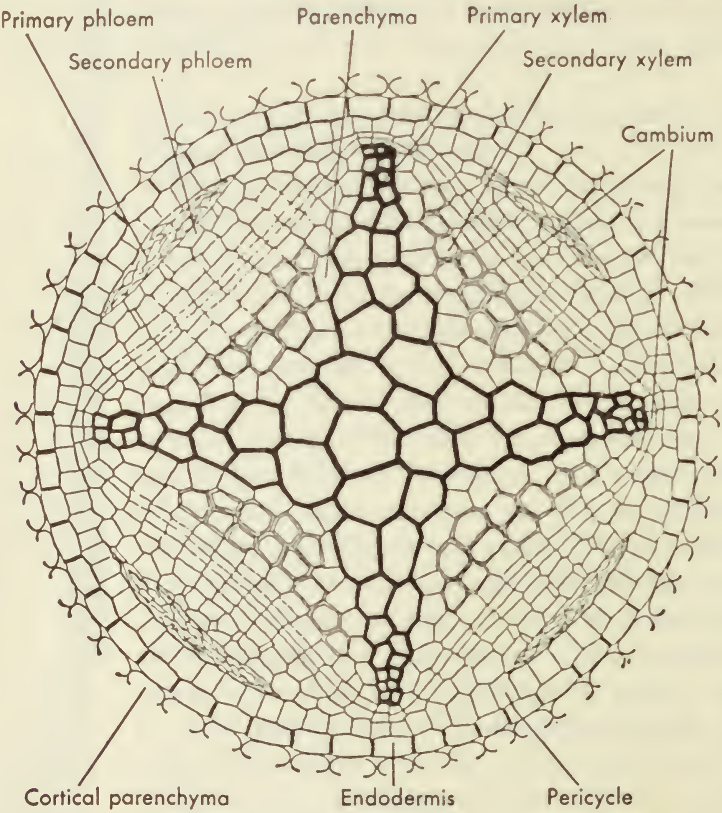

Fig. 15:6 Cross section of the stele of a dicotyledonous root at a level at which the cambium has become a continuous sheath and considerable amounts of secondary tissues have been produced. Somewhat diagrammatic. From Smith, Gilbert *et al.*, *A Textbook of General Botany*, The Macmillan Company.

from the cambium. In a cross section made somewhat back of the mature region of the root tip (Fig. 15:6), the cambium forms a continuous ring between the xylem and the phloem. The tissues formed by the cambium are called **secondary tissues.** On the outer side of the cambium **secondary phloem** is formed; on the inner side **secondary xylem.** As the root grows older the secondary xylem and secondary phloem, which come to occupy the greater portion of the stele, form two concentric masses separated by the cambium. As the root grows thicker, at certain places in the cambium, cells arise which become neither xylem vessels nor phloem tubes, but instead form parenchymatous strands extending radially between the cells of the xylem toward the center and between the cells of the phloem toward the periphery of the stele. These are the **vascular rays.**

The older roots of many plants are covered with **cork.** Certain cells, especially those of the pericycle, retain their power of cell division and differentiation and form a **secondary meristem** called the **cork cambium.** The cork cambium gives rise on its outer surface to the cork, and on its inner surface to parenchyma. The walls of the cork cells become impregnated with a fatlike substance called **suberin** which makes them impervious to water and food materials. The cells of the cortex including the endodermis, receiving no nourishment from the stele on account of the impervious nature of the cork laid down by cells from the cork cambium, die and eventually slough off, leaving the cork, the outer cells of which are also dead, as the protective layer of the root. The cork produced as described usually does not last more than a few years. In the roots of woody plants, additional cork is produced from the phloem.

2. THE STEM

We have already seen how the growth and differentiation of the tissues of the root begin at the tip of the primary root and at the tips of its branches. Similarly the growth and differentiation of the tissues of the stem begin in the buds at the ends of the stem and its branches. A **bud** contains an embryonic region similar to that in the root tip, and the region corresponding to the region of elongation in the root develops after the bud opens. Cell differentiation and growth proceed from the tip of the stem in the bud, and the youngest part of a stem or branch is the part nearest to the terminal bud, just as the youngest part of a root is the part nearest the root tip.

A. THE DICOTYLEDON STEM

We begin our consideration of the stem by studying a cross section of an alfalfa stem (Fig. 15:7) or a sunflower stem which is quite similar. Like the young root this stem is covered by a protective layer of cells, the **epidermis**. The outer portion or **cortex**, which corresponds to the

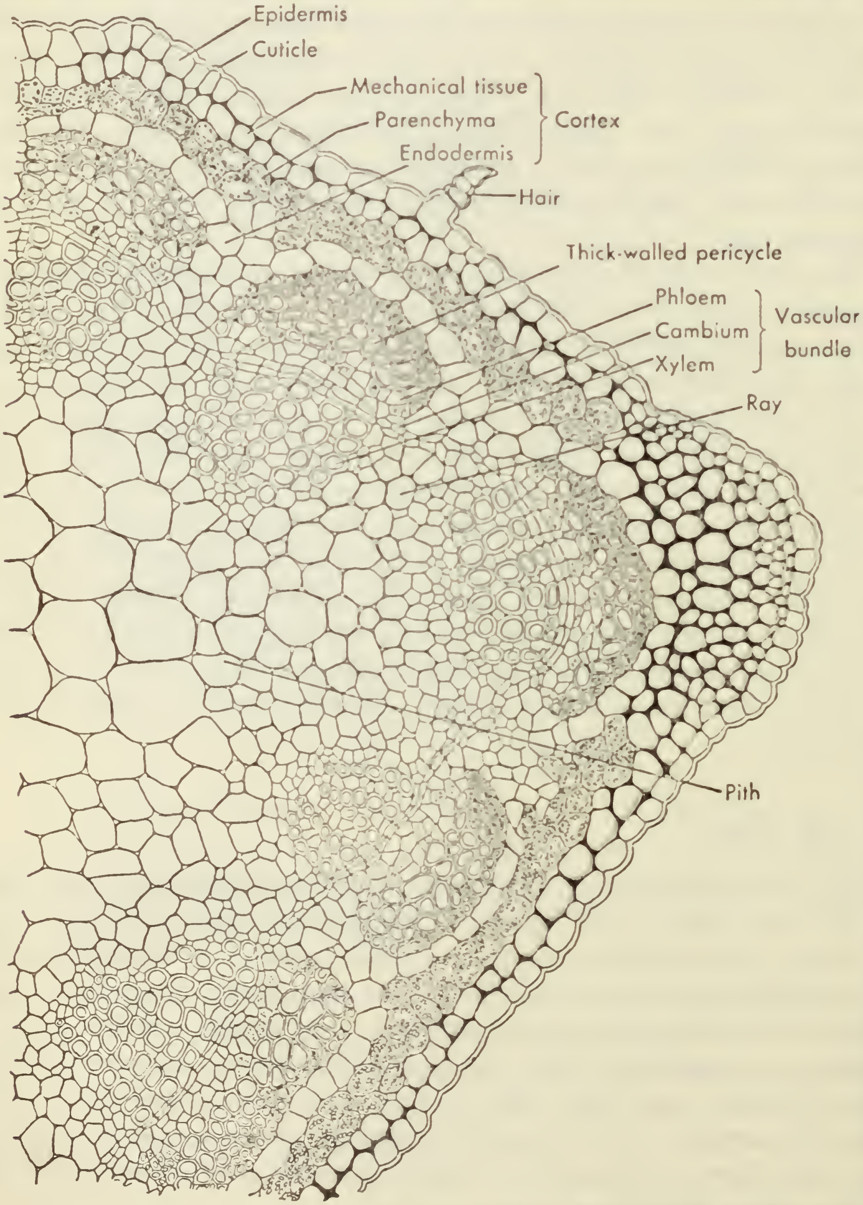

Fig. 15:7 Portion of a cross section of an alfalfa stem. From Smith, Gilbert *et al.*, *A Textbook of General Botany*, The Macmillan Company.

cortex of the root, consists of parenchyma cells and **mechanical tissue.** This latter is formed of elongated, thick-walled cells which help to stiffen the stem. The tissues of the stele of the stem present a rather different picture from the corresponding tissues of the root. The cells of the conducting tissues are grouped in a series of **vascular bundles** which are arranged in the section in a ring, leaving a large amount of pith in the central portion. Between the vascular bundles the parenchyma of the pith and cortex is continuous in the young stem and forms **pith rays** (also called **medullary rays**). In the vascular bundles the cambium lies between the phloem and the xylem, the phloem being external and the xylem internal to it as is the case in the root. A longitudinal section through a vascular bundle in the same region of the sunflower stem as the cross section shows the same tissues (Fig. 15:8).

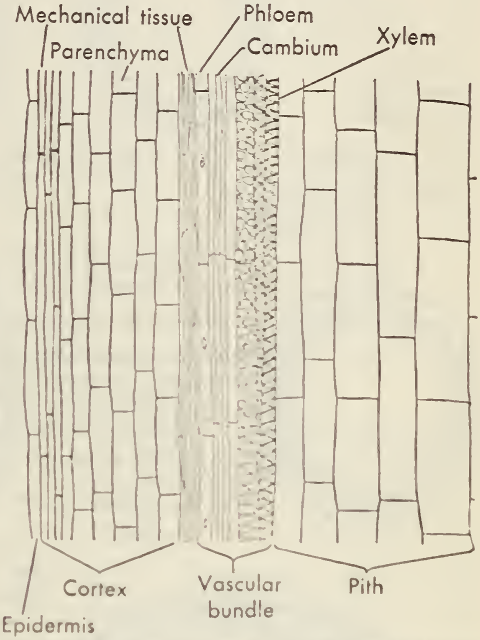

Fig. 15:8 Portion of a longitudinal section of a sunflower stem. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The structure of a tree trunk can best be understood from a study of the method of growth (Fig. 15:9). At the growing tip in the bud the cells are all alike (Fig. 15:9 A). They constitute an undifferentiated tissue called the **promeristem.** After the bud has opened and the young stem elongated the cells of the promeristem differentiate into **protoderm, ground meristem,** and **procambium** (Fig. 15:9 B). A little later these form primary tissues (Fig. 15:9 C). At this stage the vascular bundles are separate. Next **interfascicular cambium** is formed between the bundles, so that the cambium takes the form of a complete hollow cylinder (Fig. 15:9 D). Up to this time growth has been chiefly in length and only primary tissues have been developed. Now growth in length stops and the secondary tissues develop. Secondary xylem is added outside the primary xylem and secondary phloem inside the primary phloem, and the bundles extend laterally so as to form, in a transverse section, continuous rings (Fig. 15:9 E). In the cortex the cork cambium (phellogen) appears and cork is formed.

As growth continues through the years successive **annual rings** of xylem and phloem are formed (Fig. 15:9 F). The annual increase in the thickness of the xylem can usually be recognized by the fact that during the spring the xylem vessels formed are larger and have thinner walls

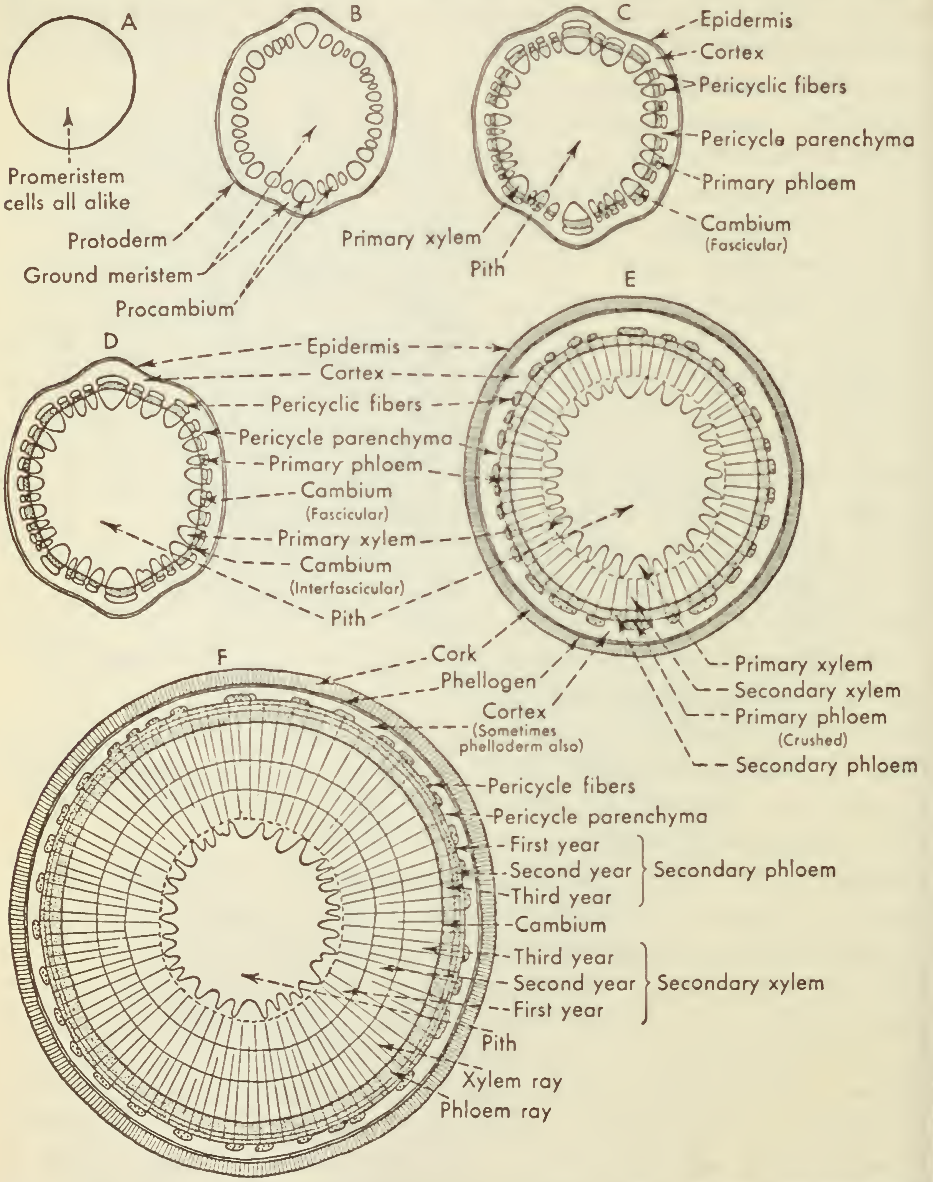

Fig. 15:9 Cross sections of the stem of an elder (*Sambucus nigra*). A, stem in a young bud; B, stem in an older bud; C, young stem; D, stem before secondary growth has commenced; E, stem in the first year of its growth showing secondary xylem and phloem; F, stem three years old. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

than those formed in the summer and fall. The older rings of phloem become crushed by being pressed against the bark as the woody cylinder of xylem increases in thickness. The formation of secondary tissues begins a few months after the growth of the stem starts and continues throughout the life of the plant which in the case of some trees may be several thousand years.

As the stem grows older the increased thickness of the xylem and phloem necessitates the development of special cells for conduction in a radial direction so that the water and other substances passing in the xylem and the phloem tubes may be distributed to the rest of the plant. These cells, which are elongated in a radial direction, i.e., in the xylem from the cambium toward the center of the stem and in the phloem from the cambium toward the cortex, form the **vascular rays,** xylem rays, and phloem rays. The vascular rays are similar in position to the pith rays found in herbaceous stems but their origin, from the cambium, and the structure of their cells, elongated radially, are quite different. The cells of the vascular rays contain living protoplasts which may remain alive in the case of large trees for hundreds of years.

In the three-year-old stem of the elder (Fig. 15:9 F), cork is beginning to form. In the stem, the process is similar to that which occurs in the root. Certain cells of the cortex just within the epidermis become active and form the **cork cambium** or phellogen. The cells of the cork cambium, by divisions parallel to the outer surface, give rise to cells which form cork. The cell walls of these cells become impregnated with suberin, which makes them impervious to water and their protoplasmic contents die. When this occurs the cells of the epidermis die and slough off leaving the cork as the outer protective layer of the stem. New cork is formed internal to the old cork by cells of new cork cambium. As the stem grows in thickness and its circumference increases the outer layers of cork often split, giving to the outer surface of the bark the roughness seen on many trees. The cork of commerce is obtained from the bark of a species of oak (*Quercus suber*).

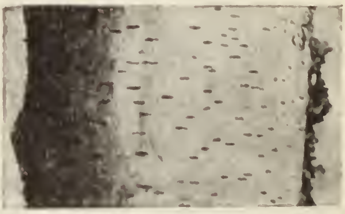

Fig. 15:10 Portion of a birch stem. The small, horizontal, dark areas are lenticels. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

In the young stem the gases of the atmosphere, oxygen and carbon dioxide, pass to the cortex and underlying tissues through openings in the epidermis, called **stomata,** and described in detail in the section on the leaf. When, however, cork with its impervious cell walls is formed special provision for the exchange of gases becomes necessary. It takes the form of **lenticels.** These are conspicuous on the bark of the birch and cherry (Fig. 15:10). When a lenticel is formed the cork cambium, instead of forming cork, forms a mass of thin-walled cells with air spaces between them.

The part of a tree between the wood and the cork, which includes the vascular cambium, phloem, cortex parenchyma, and cork cambium, is the part that is most actively alive and the part from which new tissues spring.

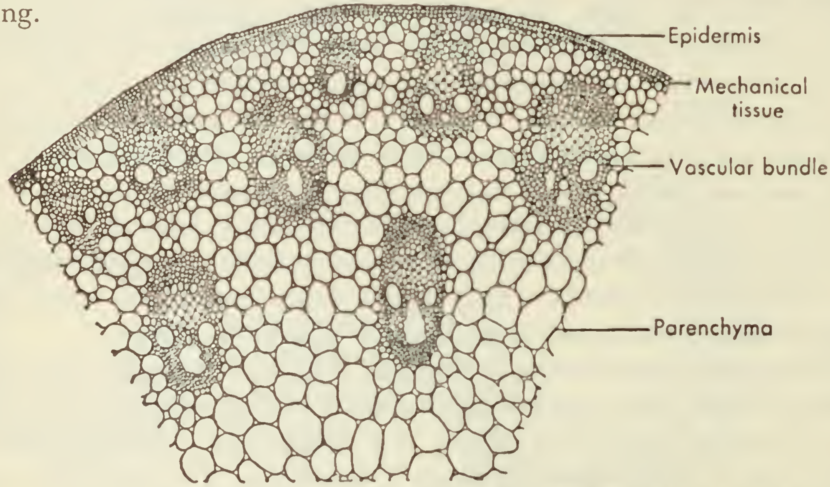

Fig. 15:11 Cross section of a corn stem. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

B. THE MONOCOTYLEDON STEM

The stems so far considered in this section are those of dicotyledons. In the stems of monocotyledons the vascular tissue occurs in vascular bundles scattered throughout a parenchyma in which it is not possible to distinguish pith and cortex (Fig. 15:11). The vascular bundles contain only primary xylem and phloem and no cambium. There is, therefore, no increase in the thickness either of the vascular bundles, or of the stem as a whole except as the individual cells may increase in size. Thus in most palm trees the stem is approximately uniform in thickness from the ground to the growing point at the top where all growth occurs and all new leaves are formed.

3. THE LEAF

It is in the leaves (and in some cases other chlorophyll-bearing structures, such as the stem) of green plants that the manufacture of food substances occurs. This is why the leaves of a plant are so important to it and why when its leaves dry up or are killed a plant will often die.

A. EXTERNAL FEATURES

Leaves vary greatly in size and shape from the tremendous leaves of some palms and tropical herbs to the minute scalelike leaves of some cedars or from the long blades of the corn plant to the small needles of the pine. A typical leaf (Fig. 15:12) may be divided into three parts — the blade or **lamina** which is the flat expanded portion, the stalk or **petiole,** and the **base** or region of attachment which is usually broader and thicker than the petiole. Often there are present small leaflike structures on either side of the base called **stipules.** The upper surface of the blade is called the **dorsal surface,** the lower, the **ventral surface.** The blade of the leaf may be either **simple** like that of the sunflower or divided into leaflets like that of the horse chestnut which is said to be **compound.** Intermediate between these are **lobed leaves** such as those of the oak or maple. Almost all of the common gymnosperms, like the pine, have narrow needlelike leaves. The **margin** of the leaf blade may be smooth or toothed. Running through the blade can be seen a network of **veins.** These consist of **vascular bundles** or portions of the stele of the stem containing xylem and phloem cells. The veins are especially well seen in the leaf skeletons often found on the ground in the late autumn. The arrangement of the veins in a leaf is called **venation.** In most monocotyledons the veins run parallel to the axis of the leaf. Such leaves are said to be **parallel veined.** In most dicotyledons the venation consists of a main vein or veins which branch repeatedly, the many ultimate fine branches being connected to form a network. Such leaves are called **net veined.**

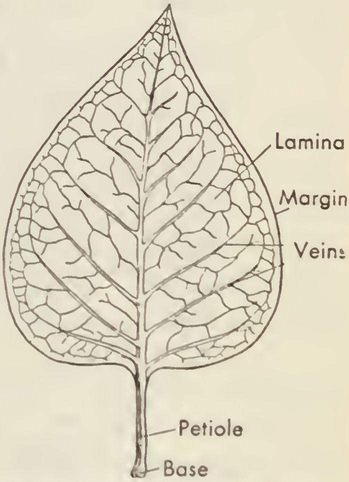

Fig. 15:12 A typical leaf. Redrawn after Chamberlain, *Elements of Plant Science*, by permission of McGraw-Hill Book Company, Inc.

Leaves may take on other functions in addition to or in place of their function in the metabolism of the plant. In the garden pea which has compound leaves certain of the leaflets become **tendrils,** used in climbing. Certain plants, which usually grow under conditions in which they are unable to get nitrogen from the soil, have, like the pitcher plants, or the Venus's flytrap (*Dionaea*) (Fig. 2:13), leaves modified for catching and digesting insects from which they obtain nitrogen.

B. INTERNAL STRUCTURE

The internal structure of the leaf is best seen in a thin cross section, passing from the dorsal to the ventral surface (Fig. 15:13). Covering the dorsal surface of the leaf are the cells of the **upper epidermis,** covering the ventral surface the cells of the **lower epidermis.** The exposed cell walls of the epidermal cells contain a substance called **cutin** which makes them less permeable to water and prevents the drying up or wilting of the leaf. The epidermal cells are without chloroplasts, except in the guard cells to be described. In the lower epidermis and less frequently in the upper epidermis are slitlike openings or **stomata** (singular, **stoma**) which lead into **intercellular air spaces** within the leaf. Each stoma is surrounded by two **guard cells,** one on either side. These guard cells, which are sausage-shaped and lie side by side with their ends in contact, are so arranged that when the air about the leaf is humid and the cells swollen the stomata are open, while when the air is dry and the cells shrunken, the stomata are closed.

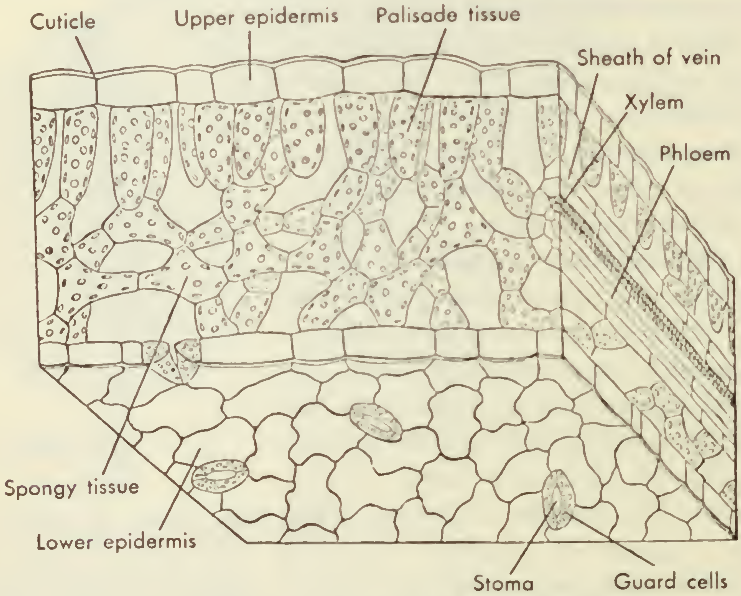

Fig. 15:13 Portion of the blade of a sunflower leaf. From Smith, Gilbert, *et al.*, *A Textbook of General Botany*, The Macmillan Company.

The greater part of the interior of the leaf is occupied by the **mes-**

ophyll, a tissue composed of cells containing chlorophyll and loosely adherent to each other. Immediately under the upper epidermis the mesophyll takes the form of **palisade tissue,** the cells of which are elongated and arranged side by side perpendicular to the surface of the leaf. These cells contain abundant chloroplasts. The rest of the mesophyll is composed of **spongy tissue,** in which the cells are irregular in shape and surround the intercellular air spaces which communicate with the exterior through the stomata. The air within the intercellular air spaces is saturated with water vapor. A thin film of water adheres to the walls of the mesophyll cells bounding the spaces. Extending through the spongy tissue of the mesophyll are the veins. Each of these consists of a **vascular bundle** composed on the upper side of xylem and on the lower side of phloem. Although the larger veins contain tracheids, sieve tubes, and companion cells, the finest branches of the veins contain only tracheids, and at their extreme ends may be represented by a single tracheid. Many of the cells of the palisade and spongy tissues are a considerable distance from a sieve tube. The sugar formed in these cells is transferred to the sieve tubes by the **border cells.** These latter cells are elongated parenchyma cells, without chlorophyll, lying lengthwise along the course of the smaller veins and in contact with the sieve tubes.

Leaves begin their development in buds. There is no secondary growth in leaves as occurs in roots and stems. The whole of the leaf is formed from the embryonic region of the bud and gradually grows equally throughout its whole extent until it reaches its full size.

4. THE STRUCTURE OF THE PLANT AS A WHOLE

In considering the cellular structure of the root, stem, and leaf, we must not lose sight of the structure of the plant as a whole. This is shown diagrammatically in the figure (Fig. 15:14). The root of the plant grows in length in the region of elongation at the tip of the main root and the tips of its branches. The stem grows in length when the buds open at the tip of its main axis and at the tips of its branches. Growth in thickness is due to the cambium which extends as a hollow cylinder through the root and stem and their branches. This growth in length and thickness occurs throughout the life of the plant, but is more active during spring and summer.

The conducting tissue extends throughout the plant in the form of two hollow cylinders, the xylem on the inside of the cylinder of cambium and the phloem on the outside.

In a woody plant the living cells are mostly confined to the root tips, buds, cambium, phloem, and leaves.

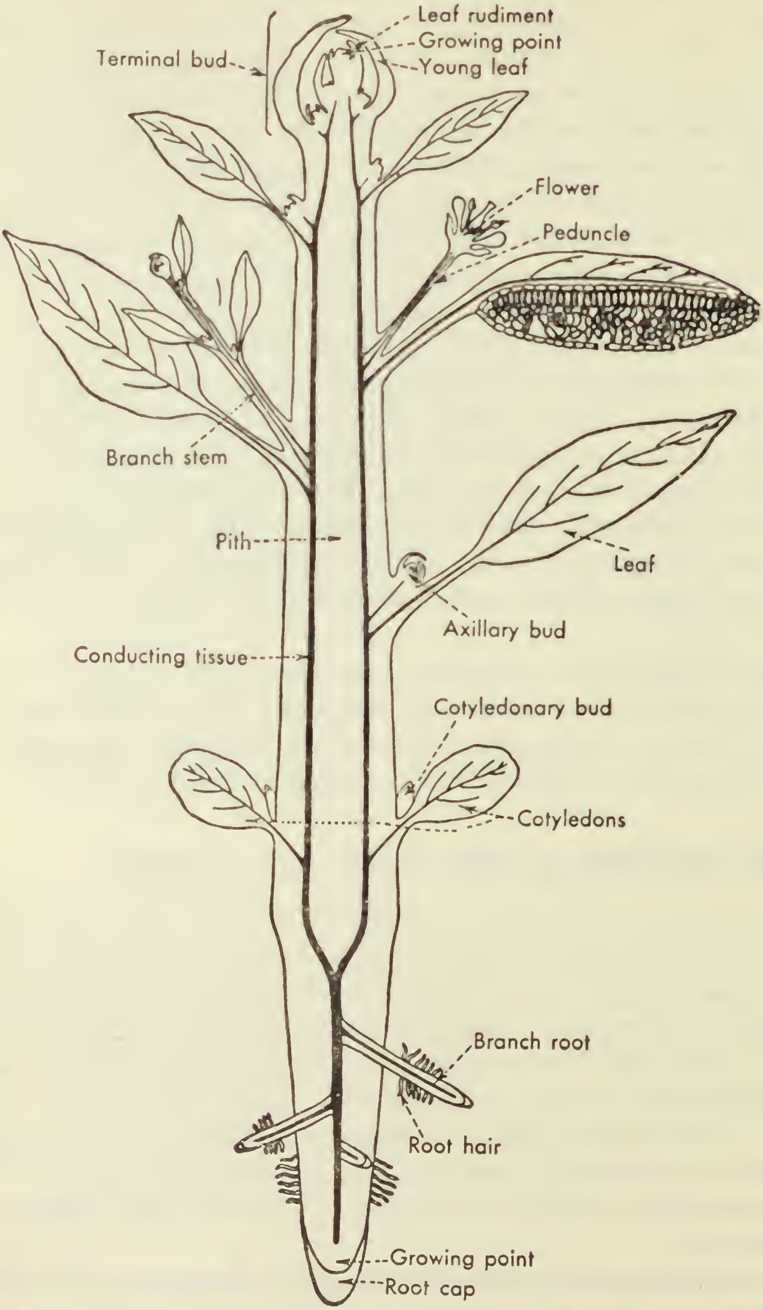

Fig. 15:14 The principal organs and tissues of a typical herbaceous plant. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

Topical Outline of Chapter 15

1. The root 320
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Questions

1. Name the four regions distinguishable in a root tip and state in general what cell activities are characteristic of each region.
2. How would one distinguish an embryonic region? What is cell differentiation?
3. How does a tracheid differ from a vessel and how do these two differ from a sieve tube?
4. What in the stem corresponds to the root tip?
5. Describe how a tree grows in thickness and how it grows in height.
6. In what parts of the root, stem, and leaves are living cells to be found?
7. At what points does growth occur in a spermatophyte?
8. In what ways is the sporophyte of a spermatophyte, such as any of those studied, adapted to life on land?

Suggestions for Further Reading

Coulter, J. M., and C. J. Chamberlain, *Morphology of the Angiosperms*, D. Appleton & Co., New York, 1903.

Holman, Richard M., and Wilfred W. Robbins, *A Textbook of General Botany* John Wiley & Sons, Inc., New York, 1934.

CHAPTER 16

Plant Physiology

The preceding chapter dealt with the structure of the root, stem, and leaf, or collectively the vegetative organs of a higher plant. The present chapter will be devoted to a consideration of the functions carried out by these organs of the plant, or to plant physiology. The vegetative organs are concerned with the absorption of raw materials, the manufacture, distribution, assimilation, and storage of food materials, used to build up the tissues of the plant, and the energy changes which these processes involve.

The raw materials used by plants are in their immediate surroundings, in the water of the soil, usually referred to as the soil solution, and the gases of the atmosphere. These raw materials include **water, inorganic salts,** and the gases **oxygen** and **carbon dioxide.** The water and inorganic salts are obtained from the soil solution by the root hairs and the epidermis of the root tip; the carbon dioxide from the atmosphere, mainly by the leaves.

Most plants, including all of the higher plants, require oxygen for respiration. This they obtain from the air, either that in the atmosphere above ground or that in the air spaces in the soil. In young stems and leaves oxygen enters the air spaces through the stomata, in older stems through lenticels (Fig. 15:10), and in the root tip through the epidermis and the root hairs.

1. ABSORPTION OF WATER

In the ground the root hairs are intimately in contact with the small particles of which the soil is composed (Fig. 16:1). Even in relatively dry soil there is always a film of water over the individual grains of earth. It is from this film that the root hairs absorb moisture. Water passes easily through the cell walls and plasma membranes of the root hairs and the epidermis of the root tip. The surface of the rest of the root is impervious to water, being covered by cells impregnated with suberin. Water on the leaves or stem of a land plant is not absorbed. An important factor in the absorption of water is the osmotic pressure within the cells. If this is greater than the osmotic pressure of the soil water, water is absorbed; if it is less, water may be lost by the root. On account of the readiness with which water passes through the cell walls and plasma membranes of root-hair cells, plants die quickly when their root tips are exposed to drying or to a solution of higher osmotic pressure than that of their protoplasm. An application of the latter principle is seen in the placing of common salt around the roots of weeds to kill them.

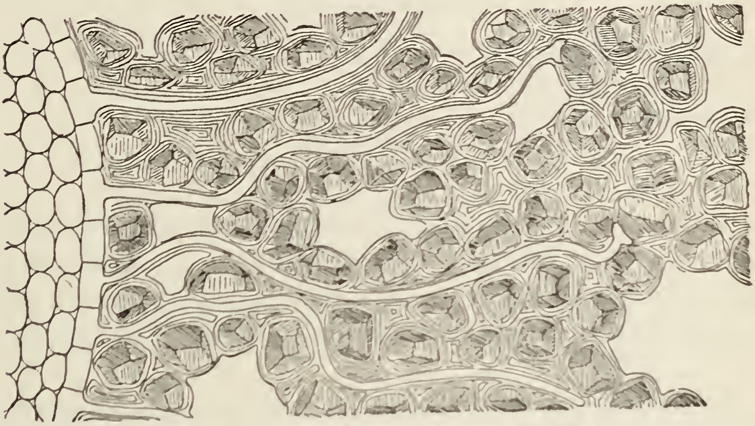


Fig. 16:1 Diagram showing relation of root hairs to soil. The concentric lines about the soil particles show the distribution of water in the soil; the white areas represent spaces filled with air. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

2. ABSORPTION OF INORGANIC SALTS

Experiments have shown that a plant will grow as well with its roots in water as in soil if the water contains certain inorganic salts. Of course such a plant must be artificially supported as the root cannot carry out in water its function of anchorage and support. With its root in a solution containing the salts in Table 16:1 a plant will thrive as well as in the most fertile soil and produce an excellent yield. The same result has been obtained with certain other relatively simple solutions. It does not follow, however, that conditions are equally simple in nature. Soil water does not always or even usually contain the above salts in the proportions required by the plant. More usually it contains a variety of salts, some of which can be used by the plant, and some of which cannot, and the plant has to make the best of the situation. What the plant really requires is certain of the chemical elements contained in the above salts, namely potassium, K, phosphorus, P, calcium, Ca, nitrogen, N, magnesium, Mg, sulphur, S, and iron, Fe, combined in such a form that it can use them. It will be noticed that when the elements in water, hydrogen and oxygen, are added to this list it contains all of the elements, with the important exception of carbon, which were stated in Chap. 5 to be essential to plants.

TABLE 16:1. A SOLUTION OF INORGANIC SALTS IN WHICH A PLANT WILL GROW

SALT		GRAMS PER LITER
Calcium nitrate	$Ca(NO_3)_2$	.80
Potassium nitrate	KNO_3	.20
Potassium phosphate	KH_2PO_4	.20
Magnesium sulphate	$MgSO_4$	.20
Iron phosphate	$FePO_4$	A relatively small quantity

The inorganic salts do not simply pass with water through the plasma membrane into the cell. They may and usually do diffuse into the cell in different proportions from those in which they occur in the water of the soil.

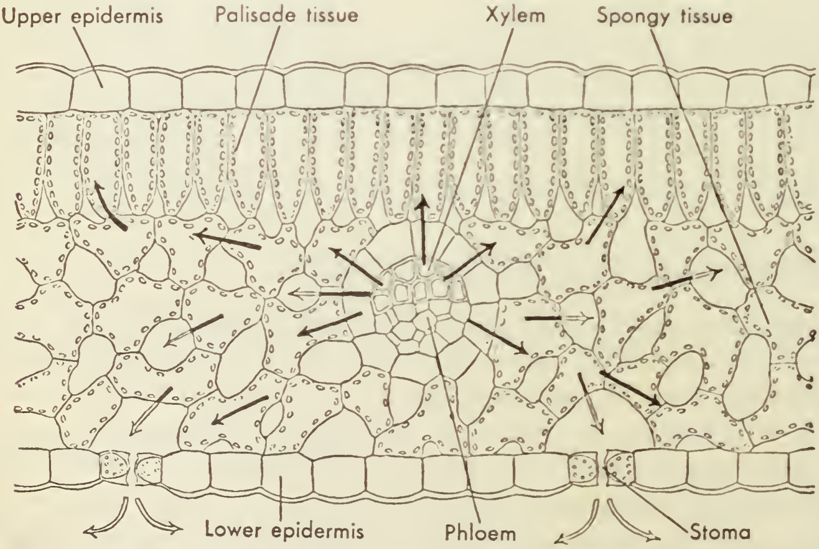


Fig. 16:2 Diagram showing the paths of movement of water through and out of a leaf. The movement of water in liquid form is indicated by black arrows; that of water in the form of vapor, by light arrows. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

3. TRANSPIRATION OR THE GIVING OFF OF WATER

Only a small portion of the water absorbed by the roots is retained in the plant; the greater part evaporates into the atmosphere, chiefly from the leaves. This process by which water is lost is called **transpiration.**

The leaf is especially adapted to facilitate and control transpiration which may be regarded as one of its important functions. The outer walls of the epidermal cells of the leaf contain cutin and are almost waterproof. Therefore only a slight amount of transpiration occurs through the epidermis. It is through the cell walls of the mesophyll cells, especially those of the spongy tissue, that transpiration occurs. The water is evaporated into the intercellular air spaces and diffuses out into the atmosphere through the stomata (Fig. 16:2). In dry weather this diffusion is more rapid than in humid weather but is controlled by the guard cells. Excessive transpiration and consequent wilting of the leaves in dry weather is prevented by the partial or complete closure of the stomata. "Under ordinary growing conditions, a square foot of the leaf surface of a sunflower transpires about four ounces of water in the course of twenty-four hours." Transpiration is the result of the permeability of the walls of the mesophyll cells to water vapor.

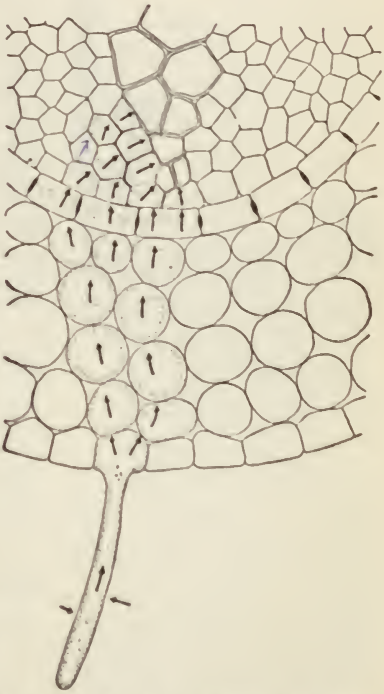


Fig. 16:3 A diagram showing the movement of water from the soil through a root hair and through the internal cells of the root to a xylem strand. From Smith, Overton, *et al., Textbook of General Botany*, The Macmillan Company.

4. CONDUCTION OF LIQUIDS THROUGH THE PLANT

The continual absorption of water by the roots and transpiration of water from the leaves produces a current of water through the plant. This current of water is carried in the conducting tissue, chiefly the xylem.

Let us trace the course of the water as it passes from a root hair to a mesophyll cell. From the root-hair cell the water passes out through the plasma membrane and cell wall to a cell of the cortex, in doing which it must pass through the cell wall and plasma membrane of the cortex cell. Why does water pass from the root-hair cell to the cortex cell? It is believed that the osmotic pressure in the cortex cell is greater than the osmotic pressure in the root-hair cell. The water passes through successive cortex cells to the cells of the endodermis. From the endodermis cells it passes to the pericycle cells. From the pericycle cells it passes to the primary xylem, in which it begins its journey upward (Fig. 16:3). From the primary xylem it passes to the secondary xylem in which it passes up through the root and stem to a leaf. The water passes through the petiole and blade in the primary xylem of the leaf. From the tracheid of a small vein it passes to the mesophyll cells of the leaf (Fig. 16:2).

This upward current of water through the plant, called the **transpiration stream,** serves to conduct dissolved salts and food materials. Usually in the spring the sap is rich in sugar. During the winter carbohydrate foods are stored in the roots and stem as starch. In the spring this is converted to sugar and diffuses into the xylem vessels.

What has been said regarding the passage of water through the plant in the xylem applies to the tallest trees. In the case of the giant Sequoia of the West, water may be moved upward a distance of over 300 feet. What is the mechanism which moves the water?

The problem of how a current of water is maintained from the tips of the roots to leaves at the ends of the highest branches of the tallest trees is an interesting one. The difference in level between the root tips and the leaves may in extreme cases reach 400 feet. Four factors have been suggested as contributing toward the maintenance of the transpiration stream. They may be stated as root pressure, transpiration, capillary attraction, and the cohesion of liquid water.

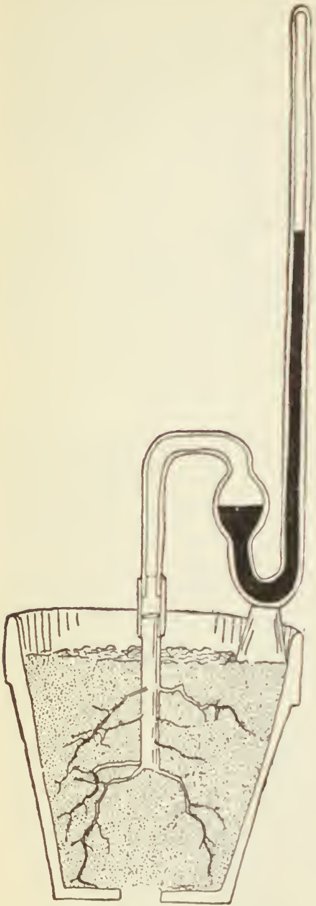


Fig. 16:4 Experiment demonstrating root pressure. The stem of a potted cutting of a geranium was cut, and its upper part was replaced by a bent closed tube containing mercury. Water exudes from the cut end of the stem, forcing the mercury upward in the tube. The top of the tube containing the mercury is closed to prevent evaporation and oxidation of the mercury. It contains air. The root pressure not only forces the mercury up but also compresses the air in the tube. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

In discussing the absorption of water by roots we have already considered the difference in osmotic pressure between the contents of the root-hair cells and the soil water. This gives rise to a **root pressure** which tends to force water upward. Root pressure can be shown by a simple experiment in which the stem is cut from a growing plant and replaced by a glass tube sealed on to the root. Water will then rise in the tube to a considerable height (Fig. 16:4).

That **transpiration** can exert an upward pull on the water in the xylem can be shown by a similar experiment. The stem of a plant which is actively transpiring is cut from its root and hermetically sealed into one end of a glass tube which is completely filled with water and placed with its other end in a glass containing mercury. Due to transpiration, water is drawn up by the plant through the glass tube and mercury enters to take its place.

Water tends to rise in any fine tube which is composed of a substance which it wets. This phenomenon is called **capillary attraction** and is explained as due to the attraction of the water molecules for those of the tube. The water in the conducting tissues of plants wets their walls.

The fourth factor, viz., the **cohesion of water,** is one with which most of us are not familiar. We ordinarily think of a thin column of water as being easily broken down and unable to resist forces tending to pull it apart. It has been demonstrated experimentally that water may show great cohesive strength and resist the pull of forces almost as great as or greater than those which would be resisted by a steel wire of the same dimensions. Thus if sufficient force is exerted by the transpiration from the leaves the water may be pulled up from the roots.

It will be remembered that while the xylem vessels are devoid of living material, the sieve tubes of the phloem contain cytoplasm and their companion cells protoplasts. The phloem is active in the transportation of food materials from their place of manufacture to their place of use or storage. This may be, and often is, downward through the stem and its branches. The medullary rays conduct water and food materials radially in the stem. The transport of food materials is called **translocation.**

5. THE MANUFACTURE OF FOOD MATERIALS

Chlorophyll is not a single substance but, apparently, is composed of two similar, rather complex, proteins referred to as chlorophyll-*a* and chlorophyll-*b*. Chlorophyll-*a* is given the formula $C_{55}H_{72}O_5N_4Mg$, chlorophyll-*b* the formula $C_{55}H_{70}O_6N_4Mg$. There is a remarkable parallel between the chlorophyll of the green leaf and hemoglobin, the red pigment which carries oxygen in the blood. The hemoglobin molecule is formed by the union of a molecule of globin, a highly complex protein, with one or more molecules of hematin, another protein. The formula of hematin is $C_{34}H_{34}O_5N_4Fe$ and resembles that of chlorophyll when iron, Fe, is substituted for the magnesium, Mg. Further, while chlorophyll acts to reduce carbon dioxide, i.e., to take oxygen away from it, one form of hemoglobin readily takes up oxygen. Since chlorophyll acts to bring about at least certain of the steps of photosynthesis, and is not itself used up in the process, it may be regarded as an organic catalyst that is an enzyme.

Photosynthesis is often represented by a simple equation:

$$\underset{\text{Carbon dioxide}}{6\,CO_2} + \underset{\text{Water}}{6\,H_2O} + \underset{\text{(Light)}}{\text{Energy}} = \underset{\text{Glucose}}{C_6H_{12}O_6} + \underset{\text{Oxygen}}{6\,O_2}$$

However, this represents only the beginning and the end of the process, which is undoubtedly quite complicated. Probably several other enzymes are involved in addition to chlorophyll. It is thought that one of the intermediate products may be formaldehyde, CH_2O. However, this substance is poisonous and must be immediately got rid of by the union of its molecules in groups of six to form glucose.

The **raw materials** required for photosynthesis are water and carbon dioxide. Water is obtained by the roots from the soil solution and passes to the cells of the leaf through the xylem. The amount of carbon dioxide in the atmosphere does not vary greatly and is normally approximately 0.03 per cent; relatively, a small proportion of the atmosphere, but absolutely, a large amount. The carbon dioxide diffuses through the stomata into the intercellular air spaces. Being soluble in water it passes into the film of water which covers the cells, lining the air spaces, and diffuses through the cell walls and plasma membranes into the cells. In pursuing this path, the carbon dioxide passes from regions of higher to regions of lower concentration.

The **energy** required in photosynthesis is received in the form of light. The leaves of a plant usually arrange themselves so as to shade each other as little as possible. Ordinary white light, such as that which comes from the sun, is a mixture of light of various colors. This can be seen if the light is caused to pass through a prism of glass or other transparent material when a spectrum extending from violet through blue, green, and yellow to red is obtained. Objects owe their color to the light which they reflect. Leaves are green because they reflect green light and also a certain amount of yellow and blue light which, when mixed, give green. The red, orange, some of the yellow, and most of the blue light go into the leaf and are absorbed by it.

Not all of the light which is absorbed by the leaf is absorbed by the chloroplasts and not all of that which is absorbed by the chloroplasts is utilized in photosynthesis. This is well shown by an experiment in which variegated leaves, i.e., leaves with white, chlorophyll-free patches, were used. Measurements obtained in such an experiment are shown in Table 16:2.

TABLE 16:2. EFFICIENCY OF THE PHOTOSYNTHETIC PROCESS

	PER CENT
Amount of energy falling on upper surface of leaf per unit of surface	100.0
Energy absorbed by green part of leaf per unit of surface	80.0
Energy absorbed by chlorophyll-free part of leaf per unit of surface	70.0
Therefore, energy absorbed by chloroplasts of green part of leaf per unit of surface	10.0
Amount of energy actually used in photosynthesis as determined from the amount of starch produced	3.5

Thus only about 3.5 per cent of the light-energy falling on the leaf is used in photosynthesis. Of the rest of the energy absorbed, part goes in transpiration and part in heating the leaf above its surroundings. The above value for the efficiency of the leaf in utilizing the sun's energy is considered to be rather high. Normally the efficiency is probably as low as 1 per cent. Inefficient as the green plant may be in utilizing the energy of the sun for the manufacture of carbohydrate food materials, man has so far been unable to devise any method which can compete with it.

The light energy is absorbed by the chloroplasts and in some way made available to produce the chemical reactions involved in photosynthesis. Photosynthesis does not occur in the absence of chlorophyll. Chlorophyll can be extracted with alcohol from a green plant leaf. However, it has not been possible to produce photosynthesis with this extracted chlorophyll; living protoplasm seems to be essential or at least certain enzymes which so far have not been isolated from protoplasm. Photosynthesis occurs only within certain temperature limits. Up to a certain point the rate of photosynthesis increases with the temperature.

To sum up, we find that for photosynthesis to occur in a living cell the following are necessary:

1. Raw materials (water and carbon dioxide)
2. Light energy
3. Chlorophyll
4. A suitable temperature

Oxygen is a by-product of photosynthesis and when the process is actively in progress, oxygen is given off by the mesophyll cells into the intercellular air spaces and diffuses out through the stomata.

Most of the sugar formed in active photosynthesis is converted almost immediately into starch. In the absence of light, as during the night, this starch may be reconverted into sugar, that is, **digested.** In the soluble form of sugar, the carbohydrate can pass into the vascular tissues and be distributed throughout the plant. Sugar is used by the plant in a variety of ways. It may be directly oxidized to **provide energy** to carry on synthetic processes other than photosynthesis; it may be turned into starch and stored in different parts of the plant as a **reserve food;** its atoms may be recombined to form cellulose for the cell walls; it may lose oxygen and its atoms may recombine to form **fats;** its atoms may become rearranged and combine with nitrogen and other atoms to form **proteins;** or lastly it may be built into the cell and become a part of the living protoplasm.

6. TRANSLOCATION

While the water and mineral salts are carried mainly in the transpiration stream, it is generally believed that translocation, or the transport of soluble organic food substances, occurs chiefly in the phloem. Evidence for this has been obtained from two sources. When a tree is girdled, i.e., when a ring of bark including the phloem is stripped from a tree, organic food materials accumulate above the girdle. Organic substances, including sugars and proteins, have been identified in the cytoplasm of the sieve tubes. Presumably translocation also occurs radially in the vascular rays.

7. RESPIRATION

The process of respiration was briefly considered in Chap 2. Respiration makes available the potential chemical energy stored in the food materials elaborated by the plant. In many respects it is the reverse of photosynthesis. In Table 16:3 photosynthesis and respiration are compared.

TABLE 16:3. COMPARISON OF PHOTOSYNTHESIS AND RESPIRATION

PHOTOSYNTHESIS	RESPIRATION
Carbon dioxide absorbed	Oxygen absorbed
Oxygen given off	Carbon dioxide given off
Carbohydrates formed	Carbohydrates used up
Energy stored up	Energy set free

While respiration takes place in all living cells at all times, photosynthesis takes place only in cells containing chlorophyll and only when they are exposed to light.

8. THE PLANT AND ITS ENVIRONMENT

The plant cannot be considered alone; its life and activities depend not only upon its own structure and inherited tendencies, but also upon its environment. All are familiar with the fact that each species of plant requires a suitable soil and a suitable climate and that differences in soil and climate produce differences in the growth and activities of the plant.

A change in any of the factors of the environment to which an organism responds by some change in its structure or activity is called a **stimulus.** The relation between stimulus and response was briefly considered in Chap. 2. Plants respond to many different kinds of stimuli. Some stimuli act in a general way on the whole organism. Such a general stimulus is heat. Up to a certain point plants tend to grow more rapidly the higher the temperature.

The term **tropism** is applied to response to a stimulus possessing direction. Examples of such stimuli are gravity and light. Response to gravity is called **geotropism.** The main or primary root of a plant grows downward and is said to be positively geotropic because the response is in the same direction as the pull of gravity. On the other hand, the stem is negatively geotropic since it tends to grow upward in a direction opposite to that of the pull of gravity (Fig. 16:5).

Response to light is called **phototropism.** Leaves and young stems are positively phototropic since they tend to grow toward the light, while roots are negatively phototropic since they tend to grow away from the light (Fig. 16:6).

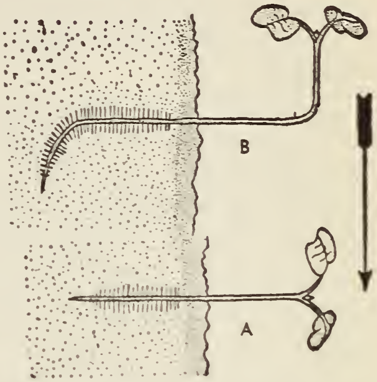


Fig. 16:5 Geotropic curvature of a seedling of mustard, *Brassica.* A, just after having been placed in the horizontal position; B, about 24 hours later. The positively geotropic root has bent downward, the negatively geotropic stem upward. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

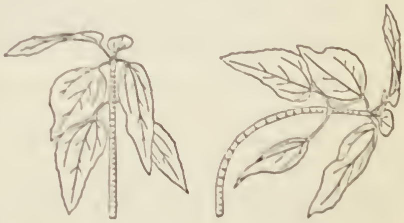


Fig. 16:6 Phototropism. On the left, part of a sunflower plant with its stem marked at equal intervals; on the right, the same plant after exposure to a one-sided illumination. The bending occurs in the region of elongation. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

Other stimuli which may exert a directive influence on plant growth are differences in the quantity of moisture. Roots tend to grow toward the more moist regions of the soil — **hydrotropism** (Fig. 16:7). Response to differences in the concentration of certain chemical substances (**chemotropism**) is exhibited by many plants, while the tendrils and young stems of climbing plants respond to contact with solid objects (**thigmotropism**).

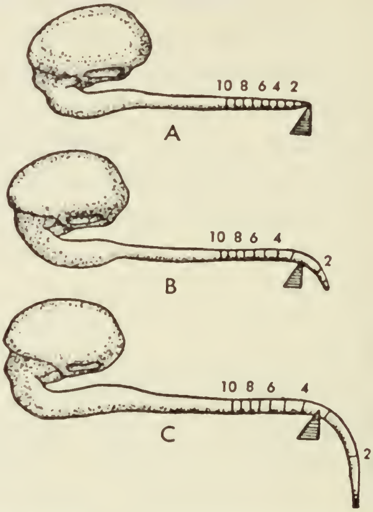


Fig. 16:8 Method of response to gravity. A seedling of white lupine, *Lupinus albus* at the time it was placed in the horizontal position (A), and after a shorter and longer period (B and C) in the new position. The end of the root is marked off into zones beginning with the extreme root tip, each originally 1 millimeter long. Note that the region of curvature corresponds with the region of most rapid elongation and that the curvature is due to unequal growth, the upper side growing more rapidly when compared with the lower. Redrawn after Sachs. From Holman and Robbins, *Textbook of General Botany*, by permission of John Wiley & Sons, Inc.

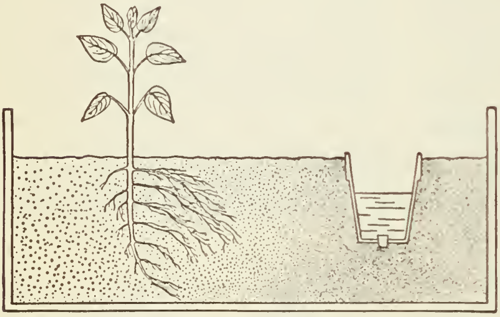
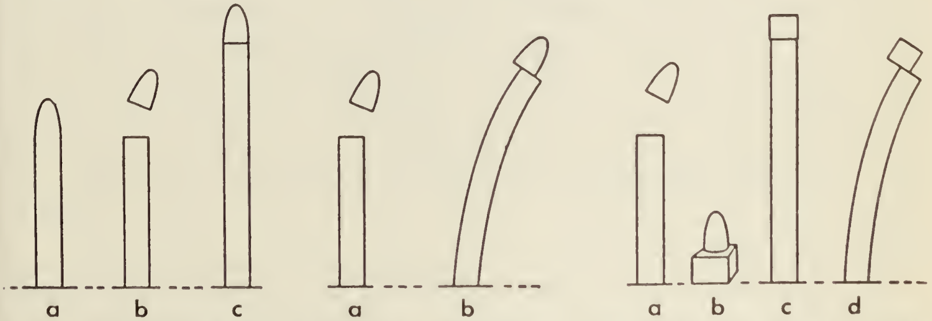


Fig. 16:7 Hydrotropism. Section of a box containing sand, with a plant near one end and a porous flower pot containing water near the other. The soil is moister nearer the pot, as indicated by the darker shading, and the unequal water content of the soil on different sides of the plant affects both the form and the direction of growth of the roots. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

The bending of the root, stem, or leaf in response to a stimulus is due to unequal growth, one side growing more rapidly and becoming convex, while the other side grows more slowly and becomes concave. If a young bean seedling in which the root has been allowed to grow straight downward in response to gravity is later turned and held so that the root is horizontal (Fig. 16:8), the part of the root formed after the turning will be directed downward. By making marks on the root it can be shown that this is due to growth being faster on the upper than the under side. That this response to gravity is not merely a falling over of the tip of the root is shown by another experiment. A germinating bean is so placed that its root floats on the surface of mercury. In spite of the mercury being about ten times as heavy as the root tip, the latter grows downward into the mercury in response to gravity.

9. GROWTH AND GROWTH SUBSTANCES

The growth of plants depends on a number of different conditions. Some of these are external to the plant such as light, temperature, availability of water and other raw materials for the manufacture of food substances. Others are internal including the heredity of the plant, the interrelations between the food and other materials in its body, and the presence or absence of certain substances designated growth substances. These growth substances seem to be of two kinds called, respectively, **vitamins** and **plant hormones.** Both substances are produced in green plants, both are effective in low concentrations. Plant hormones are formed by the plant in certain specific cells and produce specific effects when transported (presumably by translocation) to other specific cells. Vitamins seem to be produced more generally in plants and to produce more general effects.[1]



A. Effect of removing and replacing tip.
- **a.** Normal coleoptile.
- **b.** Tip removed. Growth retarded.
- **c.** Tip replaced. Growth resumed.

B. Effect of replacing tip on one side.
- **a.** Tip replaced on one side.
- **b.** Side with tip grows faster curving coleoptile.

C. Growth hormones can be transmitted through agar jelly.
- **a.** Tip removed from coleoptile.
- **b.** Tip placed on block of agar jelly.
- **c.** Agar block placed on cut-off coleoptile. Growth resumed.
- **d.** Agar block placed on side of cut-off coleoptile. Side grows faster curving coleoptile.

Fig. 16:9 Experiments showing the existence and method of action of growth hormones in plants.

The nature of plant hormones can be shown by a series of experiments. The young seedling of the oat, *Avena*, has proved a favorable object for these experiments. The **seed of the oat,** which is a monocotyledon, shows a structure very similar to that of corn (Fig. 14:20). The seeds are germinated and the growth of the coleoptile studied. This, it will be remembered, is the caplike structure which covers the epicotyl and the immature foliage leaves. The **coleoptile** is particularly favorable for the study of cell growth because cell division in it stops soon after germination, and its further growth is entirely by cell elongation, which occurs most actively toward the base of the coleoptile. (Fig. 16:9)

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[1] The effects of vitamins on animals are discussed in Chap. 29.

When the extreme tip of the coleoptile is cut off, growth of the remainder of the coleoptile is slowed. However, if the cut-off tip is later replaced, the rate of growth is increased. If the extreme tip is cut off and the cut-off end placed on one side of the cut end of the coleoptile, instead of growing vertically upward the coleoptile bends away from the side on which the tip is placed, showing greater growth on that side. These experiments and others of a somewhat similar nature suggest that some growth-promoting substance passes downward from the tip. When the cut-off tip of a coleoptile is placed on a small block of agar jelly for a short time and the block is then placed on the cut surface of a coleoptile from which the tip has been removed, results similar to those obtained by replacing the tips are obtained. This seems to indicate that some substance was absorbed by the agar jelly from the cut-off tips which was later transferred to the coleoptiles and stimulated them to grow. The term **auxins** has been applied to the plant hormones involved in experiments such as these. Three different auxins have now been isolated and their chemical composition and structure determined. All three are organic acids. One of them, auxin *a*, has the composition $C_{18}H_{32}O_5$. Strangely enough, this auxin seems to occur also in human urine.

It has been shown that auxins are effective in promoting the unequal growth in the phototropism of the stem and the geotropism of the root.

10. THE PHYSIOLOGY OF THE PLANT AS A WHOLE

We must not forget that the different physiological processes outlined in the foregoing sections of this chapter do not proceed independently. Transpiration is dependent on absorption and conduction; photosynthesis is dependent on the conduction of water to the leaves; growth is dependent on the manufacture and distribution of food materials.

The physiological activities of a plant are illustrated diagrammatically in Fig. 16:10. In studying this diagram certain facts should be kept in mind and should be emphasized. Respiration occurs in all the living parts of the plant and is most active when there is the greatest physiological activity. Growth occurs not only at the tips of the roots and the end of the stem, but wherever the cambium layer is active. Protein synthesis probably occurs in many different parts of the plant. Food may be stored anywhere in the plant body depending on the species of plant.

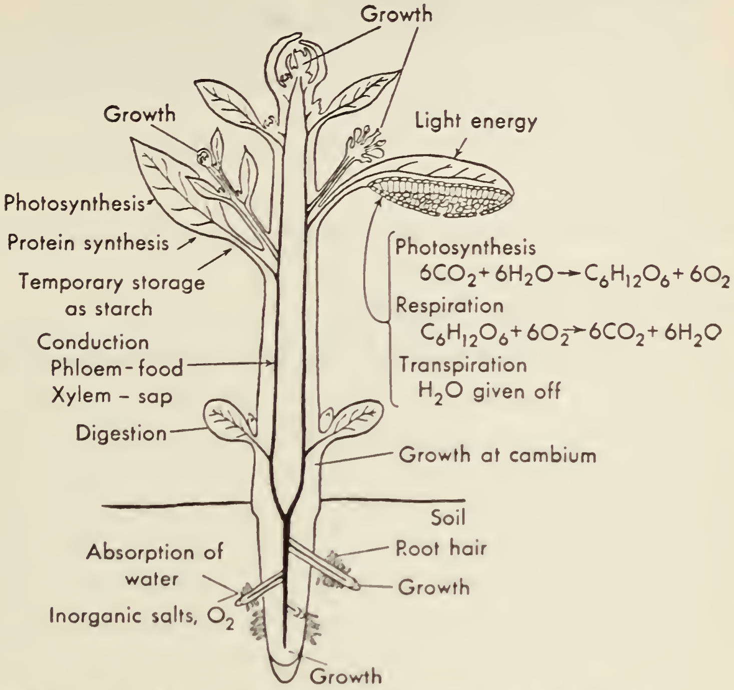

Fig. 16:10 The main physiological activities of a green plant.

Topical Outline of Chapter 16

1. Absorption of water 338
2. Absorption of inorganic salts 339
3. Transpiration or the giving off of water 341
4. Conduction of liquids through the plant 341
5. The manufacture of food materials 343
6. Translocation 346
7. Respiration 346
8. The plant and its environment 347
9. Growth and growth substances 349
10. The physiology of the plant as a whole 350

Questions

1. List the raw materials used by a plant in building up its tissues. State the source of each and where it enters the plant.
2. Show how transpiration is controlled in a plant.

3. Trace the path of a drop of water from the time of its absorption by a root hair until it reaches the atmosphere by transpiration from a leaf.
4. In the case of the above drop of water discuss the physical forces which are known to act on it during its passage.
5. Discuss the manufacture of sugar by photosynthesis; list the raw materials, giving the source of each, the by-products and their distribution, and the source of energy for the chemical changes. How efficient is the process?
6. Compare respiration and photosynthesis.
7. Give a list of stimuli and state some of the ways in which plants may respond to them.
8. What is a tropism?
9. Describe experiments showing the presence of growth hormones in plants.

Suggestion for Further Reading

Raber, Oran, *Principles of Plant Physiology*, The Macmillan Company, New York, 1933.

CHAPTER 17

The Economic Importance of Plants

1. THE IMPORTANCE OF PLANTS TO MAN

The word "botany," which is from a Greek root meaning "to feed," is eloquent testimony to the primary stimulus to the study of plants in all ages. All animals, and man is no exception, are dependent ultimately on plants for their food. Even peoples who, like some of the Eskimos, live entirely on a meat diet, feed on animals which are dependent on plant life for their food. Plants are, therefore, of the greatest economic value to man and no country or nation is capable of independent existence which does not grow the plants on which it subsists. Plants are essential not only as food but, as can be seen from the following sections, for the whole fabric of our present civilization which is dependent on the use of plant products.

2. THE CULTIVATION OF PLANTS

The cultivation of plants began in the Stone Age of man and may have arisen as the result of a happy accident, when seeds gathered for food, but accidentally scattered on the ground about the dwelling, were seen to give rise to useful plants. All the different kinds of plants now under cultivation in various parts of the world were originally obtained from wild forms although it is often difficult to say with certainty what the wild form was, and in some cases the wild forms may have become extinct. "Nearly all of the food plants of civilized man came under cultivation before the historical period; the very earliest records suggest that the grains, textile fibers, vegetables, and fruits which are now familiar to us were in everyday use" in ancient times.[1]

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[1] W. W. Robbins and F. Ramaley, *Plants Useful to Man*, P. Blakiston's Sons & Co., Inc., Philadelphia, 1933.

Agriculture did not arise independently among the primitive peoples of the world. There seem to have been three distinct areas from which both the methods of cultivation and the plants cultivated became distributed over the inhabited world: the American center of distribution, located in Central America, Mexico, and the northwest of South America; the Mediterranean center consisting of the countries bordering on the east of the Mediterranean; and the oriental region corresponding to what is now the southern half of China. In these regions the wild forms of many of our cultivated varieties can be found today.

3. THE CHIEF USES OF PLANTS

The economic importance of plants will be discussed under five headings. First, the cultivation and preservation of plants for food, which includes not only farming, but also such industries as those concerned with canning and the making of sugar. Second, the use of plants to provide raw materials for industries not directly connected with feeding the population, such as the timber, textile, chemical, and fuel industries. Third, the use of plants in medicine. Only mention can be made of the fourth and fifth, viz., the use of plants for the protection of land from erosion and desiccation, and the use of plants as ornaments, which includes the horticultural industry.

4. PLANTS USED FOR FOOD

Naturally the part of a plant used as food is the part in which it has stored nourishment in the form of carbohydrates (sugar or starch), fats (vegetable oils), or proteins. In the different species of plants these materials are stored in different parts. Thus in some cases, as in cereals, we eat the one-seeded dry fruit; in other cases the fleshy fruit as in oranges, apples, and plums; in still others, the leaves as in cabbage and lettuce; in another the stem as in the sugar cane and the potato; and in many cases the root as in the turnip, sweet potato, and beet. The botanist and the housewife attach quite different meanings to the word "fruit." For the botanist a fruit is a ripened ovary of a flower with certain floral structures with which it may be associated. The housewife applies the term only to such of the botanist's fruits as are sweet and fleshy. Thus such "vegetables" as string beans and tomatoes are, according to the botanist, fruits.

A. SEEDS AND FRUITS

(1) CEREAL GRAINS

Cereals include such plants as wheat, barley, rye, oats, corn, and rice, which belong to the family of the grasses (*Gramineae*). They form the chief food of mankind. Wheat is grown chiefly in North America and Europe, rice in the Orient.

(a) WHEAT, TRITICUM AESTIVUM

The wheat plant is a typical grass (Fig. 17:1). The stem branches underground giving rise to a number of above-ground branches called **tillers.** The leaves arise alternately at the nodes and each consists of a sheath surrounding the stem from which the leaf blade extends. Each tiller bears a single inflorescence or "ear" technically called a **spike.** The spike consists of a number of spikelets arranged on opposite sides of the main axis or rachis. A spikelet is made up of three to six flowers on a short branch or rachilla. At the base of the spikelet are two bracts, called in this case **glumes.** Each flower is in the axil of another bract

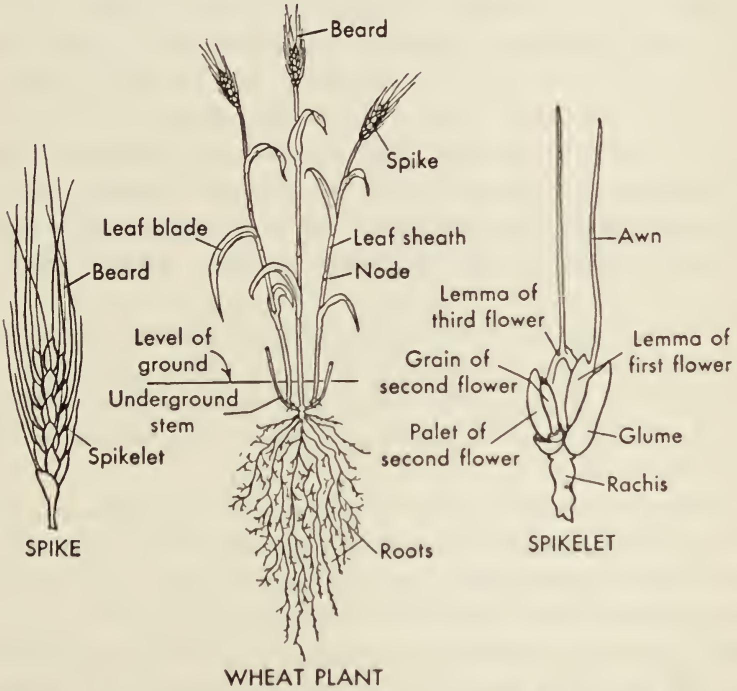

Fig. 17:1 The wheat plant. In the center the complete plant; at the left, the inflorescence, a spike; at the right, a spikelet consisting of three flowers.

called a **lemma** by which it is surrounded and almost completely enclosed. Bristles or awns on the lemmas of the flowers of the spike form the "beard" of the wheat. An individual wheat flower consists of a palet representing the calyx and two small scalelike lodicules representing the corolla. There are three stamens and a single pistil consisting of a one-chambered, one-seeded ovary and two styles, each bearing a stigma.

The fruit of the wheat is called a **grain.** It consists of the single seed surrounded by the dried-up wall of the ovary which does not split open to allow the seed to escape.

The cultivation of the wheat plant began in the Mediterranean region in prehistoric times, probably at least 2000 years before the birth of Christ. It is not surprising, therefore, that hundreds of varieties adapted to special conditions and special purposes have been developed. Some varieties produce especially large yields, others are suited to the semiarid conditions of the southwestern United States, still others to conditions on the Pacific coast. Some are best suited to the making of ordinary white flour, others produce a hard, glassy grain suited to the making of macaroni and crackers, while still other varieties make the best pastry flour.

Winter wheats are planted in autumn and produce small plants which live through the winter, develop rapidly in the spring, and ripen early in July. Such wheats can be grown only where the winters are mild. Spring wheats are sown early in the spring, and ripen two or three weeks later than the winter wheats.

The cultivation of wheat varies with the variety and the locality. It is desirable to have a rotation of crops, planting wheat one year and clover, alfalfa, or other crops for three or more years, before the next planting of wheat, because wheat takes the nitrogen from the soil.

In olden times the process of harvesting was done in several steps by hand. When the wheat was ripe the entire shoot was cut down with a sickle or scythe. This was then carried to the threshing floor where it was beaten with the flail to free the grains from the inflorescence. By winnowing, the chaff, being lighter, is blown away from the heavier grain. This is still the method used by primitive people today. On large modern farms the whole process is done automatically by a machine called a **harvester.** When made into flour the grain is ground. In whole-wheat or graham flour the entire grain is used. In the making of standard white flour the seed coat and the outer part of the endosperm are removed as the bran.

(b) BARLEY, HORDEUM VULGARE

The barley resembles the wheat plant. The inflorescence is a spike and the grain is similar to that of the wheat. The chief use of barley is in the preparation of malt. In making malt the barley grain is germinated. In this way much of the starch of the endosperm is converted to sugar. The grain is then dried and may be ground to a powder. Malt is used in preparing beverages. Barley is also grown as a pasture crop for grazing.

(c) RYE, SECALE CEREALE

Rye is similar to wheat in its structure. It will grow on poor and sandy soil, unsuited to wheat. Rye flour is used for bread. The grain is used in the manufacture of alcoholic liquors. The plant is used as a pasture crop and the dried straw is used in the manufacture of cardboard, hats, and other articles.

(d) OATS, AVENA SATIVA

The inflorescence of oats differs from that of the cereals previously considered in being a panicle. In a panicle the flowers are borne at the ends of long slender branches. Oats are largely used as food for horses. Rolled oats are used as a cooked breakfast food. The whole plant is used as a pasture crop and for making hay.

(e) INDIAN CORN OR MAIZE, ZEA MAYS

Indian corn was grown for food in South America, Central America, and Mexico long before the coming of the white man. The corn plant, *Zea mays*, resembles the wheat plant. Although much larger in size the inflorescence of the corn plant is similar in structure to that of the wheat except that in the corn there are pistillate spikes and staminate panicles. Each spikelet of the pistillate spike consists of two pistillate flowers of which only the upper one is capable of developing a seed. When ripe the pistillate spike becomes the familiar "ear of corn." The glumes, lemmas, and palets become the chaff of the corn cob. Each grain on the cob represents a ripened ovary (Fig. 14:20). The staminate panicles are longer and more slender than the pistillate spikes. The spikelets consist of two staminate flowers, each containing three stamens and an undeveloped ovary.

There are many varieties of maize. Dent corn has a smooth grain and is the variety most extensively planted in the United States. Sweet corn when ripe has wrinkled grains. In popcorn the outer seed coat is tough and resistant to loss of moisture. When heated, the grains pop due to the sudden bursting of the seed coat, which in turn is due to the steam formed from the water in the seed. Nearly every part of the corn plant can be used. The grain can be used to make corn meal, hominy, corn oil, corn flakes, starch, and glucose. Corn oil is used not only as a food, but in the manufacture of soap and paints. Cornstarch is used in the manufacture of glucose which is familiarly known as corn syrup and is sometimes used as a substitute for molasses which is made from sugar cane. It is also used in the making of gums such as those used on postage stamps and envelopes. The entire corn plant is used as fodder for cattle both fresh and after fermentation in the silo. A recent development is its use in making pressed boards to be used as a substitute for sawed lumber.

(f) RICE, ORYZA SATIVA

Rice is the great food of the Orient just as wheat is the food of the Occident. It is the chief food of the population of China and India, where meat is only rarely eaten. The rice plant is a typical grass resembling the wheat plant. Its inflorescence is a panicle like that of the oat.

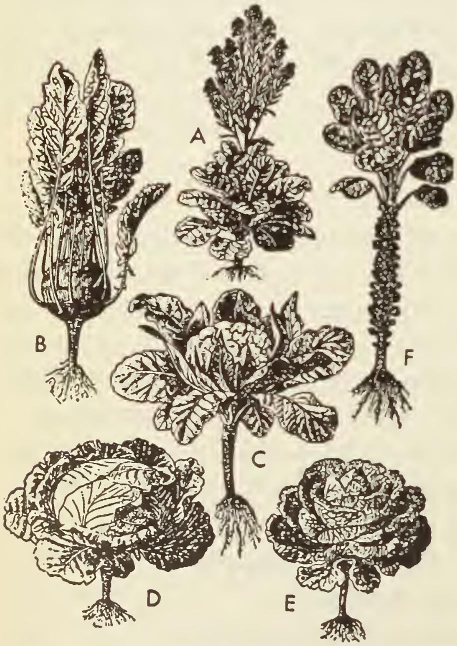

Fig. 17:2 Varieties of the cabbage. A, wild *Brassica oleracea* from which the following cultivated plants are thought to have come; B, kohlrabi; C, cauliflower; D, cabbage; E, Welsh or Savoy cabbage, F, Brussels sprouts. From Smith, Overton, *et al.*, *Textbook of General Botany*, The Macmillan Company.

(2) FRUITS

The various types of fruits are treated with examples in Chap. 14, Art. 3, where their economic importance is also discussed.

B. *LEAVES AND STEMS*

The leaves of many plants are used as a source of nourishment, vitamins, or condiments. The cabbage and its near relatives are not only important economic plants; they show in a striking way how a wild plant may be changed by cultivation. The wild cabbage, *Brassica oleracea*, is found growing at the present time on the coast of western and southern Europe (Fig. 17:2). Under cultivation this has been developed into the kale, broccoli, head cabbage, Brussels sprouts, kohlrabi, and cauliflower. In the case of kale, broccoli, and cabbage, the leaves are eaten. In Brussels sprouts, the "sprouts" are small heads which arise on the stem below the large leaves. In the kohlrabi the stem is short and fleshy and forms an article of diet in Europe and certain sections of the United States. The cauliflower is an interesting case; here it is the inflorescence which becomes fleshy and is eaten as a vegetable.

The onion (Fig. 17:3) is a biennial which forms a large bulb consisting mainly of fleshy leaf bases. In the leek, a close relative of the onion, the base of the stem and the bases of the leaves are eaten. The edible part of the endive consists of the young basal leaves. Lettuce is an annual which produces numerous leaves in a head.

The rhubarb is a perennial herb which grows up each season from a rhizome or underground stem. Large leaves appear in the spring. The stalks of these leaves constitute the rhubarb which we eat.

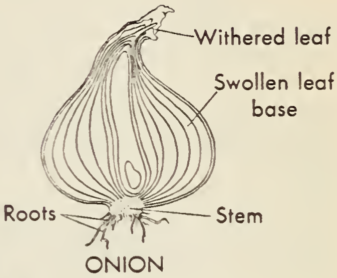

Fig. 17:3 Onion, longitudinal section showing swollen leaf bases.

The leaves of the tea and tobacco plants are in a somewhat different class from those just considered as they are not used as food. The tea plant is naturally a tree but, when grown for its leaves, is pruned down to a shrub. The leaves are about 2 inches long and leathery in texture. The tea of commerce is made from dried and broken leaves. The process involves fermentation and slow drying in the case of black tea. The chief tea-growing countries are India, including Ceylon, and China. The tobacco plant, *Nicotiana tabacum*, is an annual. When grown for its leaves the "top" of the stem where the flowers appear is cut off so that all the nourishment goes into leaf production. The large, thin leaves used for cigar wrappers are obtained by growing the plants under canvas. The shade reduces the transpiration and the development of vascular tissue.

The sugar-cane plant, which belongs to the grass family, is cultivated for the sugar stored in its stem. It is propagated artificially by planting short sections of stem from which new stems arise. The cane is passed between rollers and the juice is squeezed out. Lime is then added to the juice and unites with certain of the impurities, forming a scum on the surface and a sediment on the bottom of the containers. The clear juice is then run into evaporating pans. Here, due to the evaporation of the liquid, much of the sugar crystallizes out and is separated. The liquid which remains is known as molasses. The crushed cane is used as fuel and for the manufacture of a substitute for wooden planking.

Asparagus is a perennial herb. Early in the season fleshy shoots appear. These young shoots constitute the common table "vegetable."

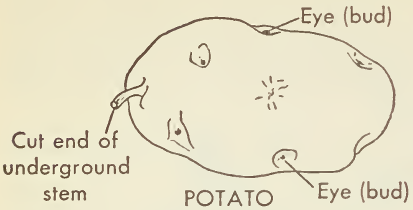

Fig. 17:4 Potato which is really an underground stem. The "eyes" are buds.

Potatoes are really swollen portions of the underground stem or tubers of the potato plant, a perennial herb. That this is so can be proved by examining the "eyes" which have the structure of buds (Fig. 17:4). Potatoes are planted by "sowing" pieces of "seed" potatoes which must each contain at least one "eye." The potato is a native of the Americas and was introduced into Europe by the Spaniards. It is second only to the cereals as food in northern countries.

C. ROOTS

About half of the world's sugar comes from the sugar beet. The other half is obtained from sugar cane. The sugar beet is a biennial herb, the fleshy root being formed during the first season. Other varieties are the garden beet, used as a table vegetable, the mangel-wurzels used for feeding stock, and the chard of which the leaves are used as "greens." Other biennial herbs, the fleshy roots of which are widely used as "vegetables," are the carrot and turnip. The radish and parsnip are either annuals or biennials depending on whether the seed is sown early or late in the season. Here also it is the root which forms the edible portion.

D. FUNGI

There are many kinds of edible fungi and some which are very poisonous. There is no general rule for distinguishing edible from inedible species. The only safe way is to know how to distinguish the individual species and to know which are edible. The mushroom most commonly seen on the market and which is cultivated for this purpose is *Agaricus campestris*. The most poisonous species belong to the genus *Amanita*. The morel, *Morchella*, is a "sac fungus" and is club-shaped. The famous French truffles, of which the commonest is *Tuber brumale*, are also sac fungi. The fruit is developed underground, usually among the roots of oak trees. French peasants use hogs, which are able to detect the fungus by its smell, in collecting the plants for the market.

Something has already been said in the chapter on thallophytes concerning the fungus diseases of plants where the life cycle of the wheat rust is described. Other important fungus diseases of economic plants are the different smuts attacking cereals, the late blight of the potato, the mildews attacking various fruits, especially that of the grape, and the apple scab. Some plant diseases, including the fire blight of the pear, are caused by bacteria, but most plant diseases are caused by other kinds of fungi.

5. PLANT PRODUCTS

Not only do plants supply the major part of man's diet but they also provide the raw materials for many important industries. Indeed, it is only necessary to look around one to see that without plant products civilized man would be without shelter, furniture, and most of his clothing, not to mention many other things which contribute to his comfort and efficiency.

A. *TIMBER*

Wood is composed almost entirely of the xylem of trees. Its rigidity is due to the xylem cells. Woods are distinguished as softwoods and hardwoods. In a softwood the xylem vessels are large and relatively thin walled, while in a hardwood the vessels are usually smaller in diameter and have thicker walls. Most of the trees which yield soft woods are Gymnosperms and the most important of these are the various varieties of pine (*Pinus*). White pine, on account of the ease with which it can be worked and the absence of warping and splitting, was one of the most important of woods. Of late years the supply of this wood has become reduced and other species are taking its place. Two species of true spruce (*Picea*), and the so-called Douglas fir (*Pseudotsuga*), are in common use. Of the hardwoods the different species of oak (*Quercus*) are most important. Three widely used species of oak are white oak, red oak, and live oak, the first being the most important and useful. Other important hardwoods are: whitewood (from the tulip tree), maple, elm, ash, and chestnut. For the making of furniture, walnut, cherry, birch, and oak are important among woods growing in this country while imported woods such as mahogany, rosewood, and satinwood are the most prized.

The cork of commerce is obtained from the cork oak (*Quercus suber*), a Mediterranean tree. Besides timber and cork a number of other important products used in industry are obtained from trees, such as rubber, turpentine, and wood alcohol. Rubber is obtained from the sap of a number of different tropical trees, the most important being the Para rubber tree (*Hevea*). Turpentine is obtained by distilling the sap which exudes from many trees. The material left behind in the distillation is called **resin.** Resins are used in the making of varnishes.

Wood pulp, as used in papermaking, is made chiefly from soft woods. Wood chips and sawdust are now used extensively as a source of cellulose which is treated chemically to produce a great variety of artificial fibers and films used for a variety of purposes.

B. TEXTILES

Three plants are especially important in the textile industry, cotton, flax, and hemp. Cotton is obtained from a number of different species of plants, some originally trees or shrubs which by cultivation have been developed into low herbaceous forms. The fruit of the cotton plant is a capsule containing numerous seeds. The capsule opens when ripe and is then called a **boll.** Each fiber of the cotton is a hairlike outgrowth of a single cell of the epidermis of the seed coat. Two kinds of hairs occur, long hairs which form the "lint" and short hairs which form the "fuzz." More than half of the world's annual production of cotton comes from the southern states of the United States. The cotton bolls are picked by hand from the cotton plant, and formerly the lint was picked from the seeds also by hand. The cotton gin has replaced hand labor for picking the lint. It consists of a series of small saws which automatically remove the long fibers or lint from the seeds. For the market the cotton is tied in bales weighing approximately 500 pounds each. The lint is spun into thread and woven into fabrics. Cotton is also used as a source of cellulose for the making of guncotton, celluloid, and rayon.

The flax plant is an annual about 2 feet high with small narrow leaves. It has been cultivated from early times in Europe, Africa, and Asia but is unknown in the wild state. The flax of commerce is obtained from the stem, each fiber being an elongated cell of the mechanical tissue of the cortex. The preparation of the fiber from the stem includes exposure to the weather for several weeks which brings about a partial separation of the fibers from the other tissues. The final separation is brought about by a fermentation process called **retting,** in which the fibers being more resistant remain after the decay of the other parts. This is followed by treatments which serve to further separate and clean the fibers. The fibers are spun into linen which may be used either as thread or woven into cloth. Linseed oil is made from the seed of the flax.

The hemp plant is an erect annual from 5 to 12 feet high. The fibers like those of the flax are cells of the mechanical tissue of the cortex of the stem. The process of preparation is somewhat similar to that of flax. The fibers are coarser than those of the flax plant and are spun into ropes and twine and woven into canvas.

C. FUELS

Nearly all fuel comes either directly or indirectly from plants. Coal is fossilized plant material. Peat is dried, decayed vegetable material from bogs.

6. MEDICINAL PLANTS

The search for medicinal plants began before recorded history and has continued to the present day. This search has had many interesting phases and its history throws light on man's efforts to combat disease.

During the Middle Ages there developed an interesting superstition called the **doctrine of signatures.** According to this doctrine there was a correspondence between the shape of a plant and the organ of the human body which it affected. Thus, it was believed that a plant with heart-shaped leaves would be effective in the treatment of heart disease, a kidney-shaped seed in renal disturbances, and so on.

The modern science which deals with the effect of drugs on the body is called **pharmacology.** The study of the chemical composition and physiological effects of drugs has led in many cases to the discovery of the active principles or essential substances which they contain. Directions for the preparation and identification of drugs in the United States are published in a book called the ***United States Pharmacopoeia.*** This is the standard for all drugs used in the United States. Other countries have their own pharmacopoeias.

Some plants are of special interest as the sources of important drugs. **Opium,** which is the dried juice of the fruit (capsule) of the poppy plant, is the source of a number of opiates or sedatives, the oldest and best known of which is morphine; another is codeine. Heroin is a white, crystalline substance derived from morphine. All these drugs are dangerous habit formers. **Belladonna** is obtained from the leaves and roots of the belladonna plant and contains atropine as its active principle. Atropine is used to paralyze the muscle of the iris by ophthalmologists. **Ergot** is the common name of a fungus, *Claviceps purpurea*, which causes a disease of rye and other cereals, but is also applied to a drug obtained from the fungus. It stimulates the contraction of smooth muscles, especially those of the uterus and is used to aid delivery in childbirth. **Strychnine** is obtained from the seeds of *Strychnos nux vomica*, an East

Indian tree, and other plants. It is used as a cardiac stimulant. **Digitalis,** which is the ground-up leaves of the foxglove and contains digitalin as an active principle, slows the action of the heart. **Cascara sagrada** is obtained from the bark of the California buckthorn and is used as a mild cathartic or laxative. **Castor oil,** obtained from the bean of the castor-oil plant, is another common cathartic. Very few drugs have a specific action on the parasites of infectious diseases. **Quinine,** a white powder extracted from the bark of the cinchona tree, is one of them. When taken by mouth it kills the malarial parasite in the blood stream. **Atebrin** is used as a substitute for quinine.

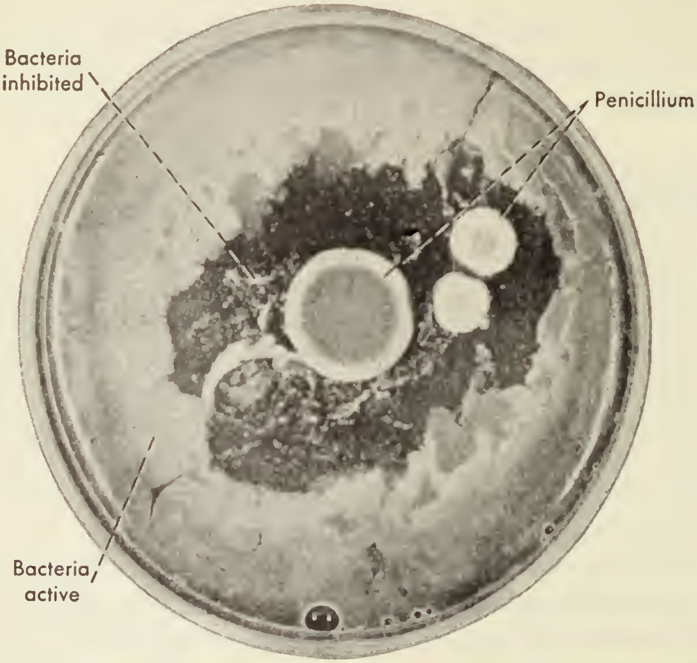

Fig. 17:5 Colonies of *Penicillium*, showing surrounding zone of bacterial inhibition. The Petri dish was first inoculated with *Staphylococcus aureus*. The bacteria were allowed to spread over the agar, forming an orange-colored film (gray in the photograph) over the whole surface. Three colonies of *Penicillium notatum* were then started on the same plate. As the colonies, which appear as circular white areas with darkened centers, grow out they are surrounded by a clear area (dark in the photograph) from which the orange film has disappeared due to the inhibition of the bacteria. This is the phenomenon, noted by Fleming in 1929, which led to the discovery of penicillin. Reproduced from *The Story of Penicillin*, Merck & Co. Inc., Rahway, N. J.

Penicillin seems to be almost ideal for combating many bacterial infections. The discovery of this remarkable substance was the result of observations made on a culture of bacteria (*Staphylococcus*) which had become contaminated by the growth of a mold. The green mold, which belonged to a common variety, *Penicillium notatum*, was seen to be surrounded by a zone in which the bacteria were disintegrating (Fig. 17:5). When this mold, a variety of *Penicillium notatum*, was isolated and grown in pure culture, it was found to produce a potent antibacterial substance which diffused into the culture medium. The antibacterial substance was then isolated in a partially pure form. During the Second World War very active research resulted in further purification and the production of the new drug on a large commercial scale. Penicillin is regarded as the best therapeutic agent available for the treatment of a number of common and serious bacterial infections including some types of pneumonia, meningitis, mastoiditis, and peritonitis.

More recently another drug called **streptomycin** similar to penicillin has been isolated from another mold, *Streptomyces griseus.* Streptomycin is the first drug found which can cure tularemia (rabbit fever) and certain dangerous and resistant urinary infections. It has also been used with some success against influenzal meningitis, typhoid fever, bacillary dysentery, and wound infection. The drug has been shown to kill the bacillus of tuberculosis in laboratory cultures but so far has not been used successfully in the human body.

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Questions

1. Discuss the origin of agriculture.
2. List the chief uses of plants.
3. Name the most important food plant in the Western Hemisphere.
4. Describe the preparation of wheat for food.
5. Give the botanical names and the uses of barley, rye, oats, maize.
6. Name the part eaten in a plum, peach, date, cucumber, apple, orange.
7. Give examples of aggregate fruits which are eaten.
8. Give two examples of multiple edible fruits.
9. What is a chestnut?
10. How are coffee and cocoa obtained?
11. Give examples of plants with edible leaves.
12. Give an example of a plant grown for the petioles of its leaves.
13. Give the source of tea and tobacco.
14. What is a potato?
15. What are the two chief sources of sugar?
16. Discuss edible fungi.
17. Name two hardwood and two softwood trees.
18. What is the source of cork?
19. Name the three most important plants grown to provide raw materials for textile industries. What products are made from each?
20. Name five drugs and state their sources.

Suggestion for Further Reading

Robbins, W. W., and F. Ramaley, *Plants Useful to Man*, P. Blakiston's Son & Company, Inc., Philadelphia, 1933.

PART III. Invertebrates

“The lower animals have not the high advantages which we have, but they have some which we lack.”

Montesquieu

CHAPTER 18

Unicellular Animals (Phylum Protozoa)

This part is concerned with the more important invertebrate phyla. We begin with the phylum which contains the simplest animals — the phylum Protozoa. The animals included in this phylum all consist of a single cell, or in certain cases of groups or colonies of single cells, each capable of carrying on an independent existence.

1. THE CLASS SARCODINA

A. AMOEBA, A UNICELLULAR ANIMAL

An amoeba is about the size of the extreme tip of a well-sharpened pencil or a little smaller than the period at the end of this sentence. It is the most famous and the best known single-celled animal. Of the many wonders which the microscope has revealed there is probably none which has had more fascination for the student. No one who has once seen its agitated grayish and transparent form gradually flow across the field of view will ever forget the sight, and the thrill of looking at and through the very essence of life, naked living protoplasm.

The outer surface of amoeba consists of the **plasma membrane,** there being no cell wall or other visible covering. The peripheral portion of the cytoplasm is clear and devoid of granules. It is called the **ectoplasm** to distinguish it from the internal granular portion of the cytoplasm which is called **endoplasm.** Some authorities distinguish in the endoplasm an inner fluid portion of the endoplasm which they call the plasmasol, and an outer gelatinous portion which they call the plasmagel, and maintain that there is a constant interchange between these two portions (Fig. 18:1).

Amoeba usually occurs on dead leaves or other objects with which the bottoms of ponds are covered. An amoeba moves over this material, which forms the substratum, by thrusting out portions of its cytoplasm, called **pseudopodia** in the direction in which it is going (Fig. 18:2). The term **amoeboid movement** has been applied to this characteristic mode of locomotion, which is regarded as probably the most primitive method of locomotion among animals. Exactly how a pseudopodium originates and exactly what is the mechanism of its movement are not clear. Two theories have been advanced. One, which may be called the **surface tension theory**, maintains that there is a lowering of the surface tension at the surface of the plasma membrane where the pseudopodium is formed leading to a bulging of the cytoplasm. Another, which may be called the **sol-gel theory**, is based on the presence of a plasmasol and a plasmagel and maintains that changes from the sol state to the gel state, and vice versa, cause the endoplasm to flow in a particular direction and form a pseudopodium. Amoeba adheres to the substratum, possibly by means of a secretion passed out through the plasma membrane.

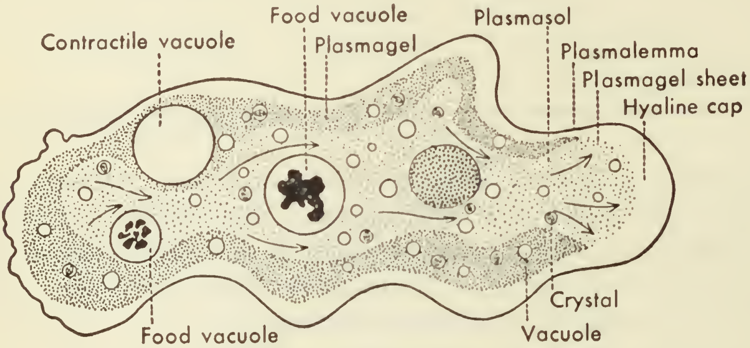


Fig. 18:1 A diagram of an amoeba illustrating the sol-gel theory of pseudopodia formation. The more liquid plasmasol is forced in the direction of the arrows by the more solid plasmagel. The plasmasol flows into the pseudopodium and changes into plasmagel at the sides. A hyaline cap is formed at the front end of the pseudopodium. The plasmalemma is a membrane which appears to be equivalent to the plasma membrane. After S. O. Mast from Hegner, *College Zoology*, The Macmillan Company.

The method by which an amoeba obtains its food resembles the method by which certain of the gastrodermal cells of *Hydra* ingest food particles which is described in Chap. 2. It feeds on other minute plants and animals which abound in the water in which it lives. These it captures by means of its pseudopodia. When an organism suitable for food is encountered, pseudopodia are thrust out around it and gradually enclose it along with a minute drop of water (Fig. 18:3). Such a minute drop of water enclosing the meal and surrounded by a portion of the plasma membrane, which now lies within the protoplast, is called a **food vacuole.** The captured organism may be still alive when taken into the food vacuole and if it is a motile form may be seen swimming around in the water contained in the vacuole.

To be used as food the captured organism must be digested. **Digestion** consists in making the nutritive material soluble, so that it can pass through the membrane lining the food vacuole into the cytoplasm of the amoeba. To become soluble the material must be changed chemically. These chemical changes are brought about in the food vacuole. Enzymes are formed in the cytoplasm of the amoeba and pass through the vacuolar membrane into the food vacuole. The nature and activities of enzymes were discussed in Chap. 7. By their catalytic action the insoluble organic materials which are contained in the food materials are broken down into simpler soluble substances. The process by which these soluble substances pass through the plasma membrane into the cytoplasm of the amoeba is called **absorption**. The material absorbed through the plasma membrane into the protoplasm is either stored in it as reserve food material or built up into new protoplasm. This latter process is called **assimilation**. Not all of the materials in the captured organism can be digested by the enzymes produced by the amoeba; some remain undigested and insoluble. After all of the digested material has been absorbed through the plasma membrane of the food vacuole into the protoplasm of the amoeba, the remaining contents of the food vacuole

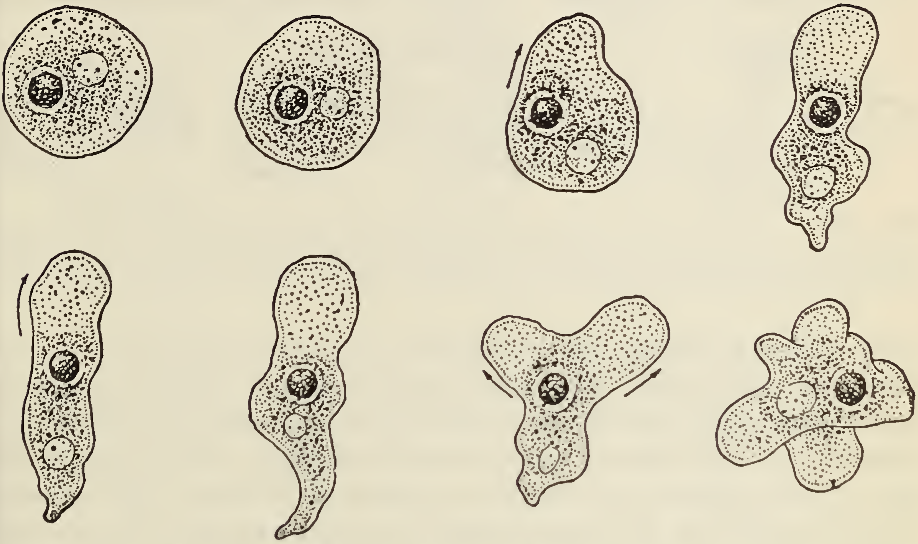


Fig. 18:2 Amoeboid movement. Successive changes in form assumed by an amoeba. The clear ectoplasm flows forward, followed by the granular endoplasm with the nucleus (darker) and contractile vacuole (lighter). Modified after Verworn, from Woodruff, *Foundations of Biology*, The Macmillan Company.

are expelled. This process of expulsion of undigested material is called **egestion.** In the case of egestion the material expelled never has passed through the plasma membrane and never really formed a part of the cell. In this respect egestion is quite different from excretion which is considered in the next paragraph.

The vital processes carried on by the protoplasm of the amoeba require energy. Energy is needed for the manufacture of the more complicated kinds of food materials, for the building up of new protoplasm, for the movement of materials within the protoplasm, and for the locomotion of the amoeba. The energy for all these activities comes from the breaking down and oxidation of food materials, especially carbohydrates and fats. To this process of oxidation as carried on in living cells we have already applied the term **respiration.** An amoeba can live only in water which contains a certain amount of oxygen in solution, which oxygen usually gets into the water from green plants during the day and from the surrounding air at all times. The oxygen in solution in the water passes through the plasma membrane of the amoeba into its protoplasm. Similarly the carbon dioxide formed in the protoplasm as a result of respiration is passed out through the plasma membrane into the water. Other materials besides carbon dioxide arise from the breaking down of food materials and protoplasm, e.g., urea which contains nitrogen. These materials are also passed out through the plasma membrane. The giving off of these materials is called **excretion.** It will be noticed that the materials given off in excretion were actually in the protoplasm and there took part in living processes.

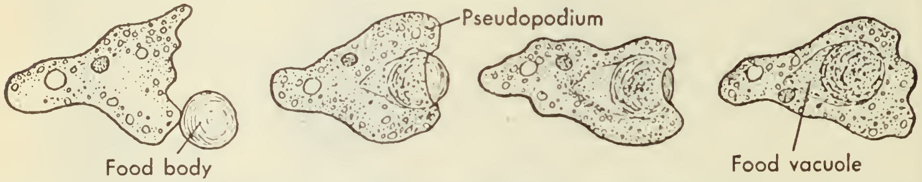


Fig. 18:3 Amoeba feeding. A series of drawings made at short intervals of an individual ingesting a cyst of *Euglena.* Redrawn after Jennings, *The Behavior of the Lower Organisms,* by permission of the Columbia University Press.

In the endoplasm of the amoeba are various small granules, which consist, in most cases, of stored food materials. If these granules are watched it will be seen that they are moved along in a continuous stream by the endoplasm. This movement makes possible the formation of pseudopodia but it is also concerned in the distribution throughout the protoplast of the materials involved in the processes of metabolism. A conspicuous structure in the cytoplasm of the amoeba is the **contractile**

vacuole (Fig. 18:1). This appears as a clear round body which periodically disappears, sending its contents, which are mostly water, to the outside. The contractile vacuole probably aids in excretion, but its main function would seem to be to relieve the protoplasm of excess water. Water is formed in amoeba as a result of respiration. It may also enter the amoeba through the plasma membrane or the membranes of the food vacuoles as a result of greater osmotic pressure within the animal. In line with this latter possibility is the fact that endamoebas, which live in the intestines of higher animals, where the osmotic pressure is relatively high, are without contractile vacuoles.

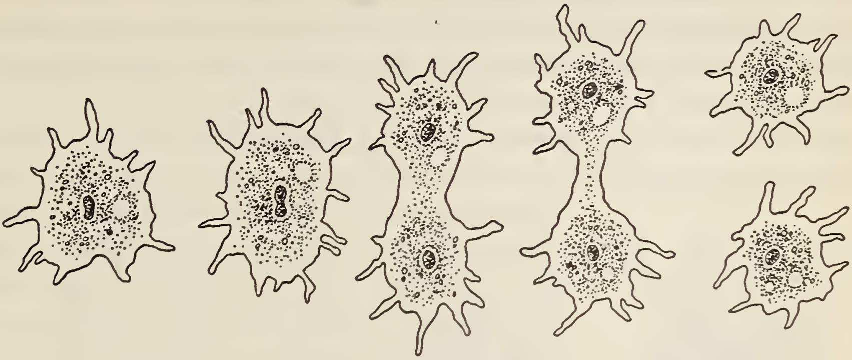


Fig. 18:4 Amoeba dividing. Redrawn from L. L. Woodruff, *Animal Biology*, The Macmillan Company.

The amoeba reproduces by **division** (Fig. 18:4). First the nucleus divides and then the cytoplasm becomes constricted and eventually divides, forming two daughter individuals which separate and grow to the size of the parent when they in turn may divide.

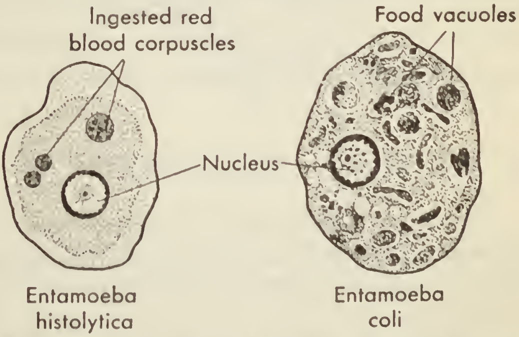


Fig. 18:5 *Endamoeba histolytica*, cause of amoebic dysentery, and *Endamoeba coli*, a harmless parasite of the human intestine, magnified approximately 850 times. Redrawn after Chandler, *Introduction to Human Parasitology*, by permission of John Wiley & Sons, Inc.

B. OTHER SARCODINA

Besides *Amoeba* which has already been described, many other interesting Protozoa are included in the class Sarcodina. Very similar to *Amoeba* are the various species of the genus *Endamoeba*, parasitic in the mouth and intestinal tract of man and many other animals. The oral endamoeba of man, *Endamoeba gingivalis,* is believed to be the cause of **pyorrhea,** a rather common disease in which the teeth become surrounded by pus pockets and may eventually fall out. One of the intestinal endamoebas of man, *Endamoeba histolytica* (Fig. 18:5), is a cause of a form of **dysentery** not uncommon in certain parts of the tropics. There is also a harmless species, *Endamoeba coli,* which occurs rather frequently in the intestine of man in all parts of the world (Fig. 18:5).

Included in the class Sarcodina are the **Foraminifera** and the **Radiolaria,** small animals of the sea, important on account of their great abundance and as food for many other marine animals. The Foraminifera form minute shells, many of which are like miniature snail shells (Fig. 18:6). Although individually microscopic, these organisms have occurred and occur in such great numbers that their shells, after sinking to the bottom of the ocean, have formed great layers of rock. The chalk of chalk cliffs is often composed almost entirely of the shells of Foraminifera. The Radiolaria include many beautiful radiate forms with siliceous skeletons. Over vast tracts of the ocean floor their skeletons are the principal, almost the sole, constituents of the ooze (or fine mud) and the same must have been true in past times since in many geological deposits the rocks are composed of the same materials.

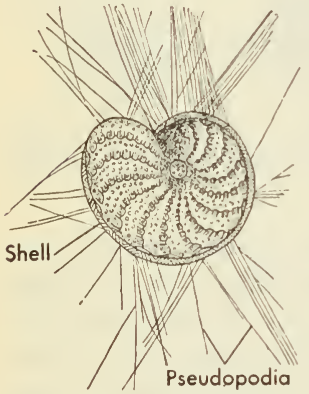


Fig. 18:6 A forminiferan (phylum Protozoa, class Sarcodina).

2. THE CLASS MASTIGOPHORA

The class Mastigophora is abundant and widely distributed, occurring in fresh and salt water, in the soil, and parasitically in animals and plants. Three examples will be described: the free-living plantlike *Euglena,* the colonial *Volvox,* and the parasite of African sleeping sickness, *Trypanosoma gambiense.*

A. EUGLENA

Euglena is a small, single-celled organism which lives in small freshwater ponds under much the same conditions as *Amoeba,* excepting that it occurs near the surface. For reasons which will appear later, it is sometimes classified as a plant. It is taken up at this point because its structure can be more easily understood after a study of *Amoeba.* The general shape of *Euglena* may be described as that of a cigar, rather pointed at one end and blunt at the other (Fig. 18:7 A). This relatively fixed shape is due to the existence of a thin elastic membrane or **pellicle,** covering the outer surface, outside the plasma membrane. The pellicle is sufficiently elastic to allow the protoplast to bend and undergo a series of contractions proceeding from one end to the other, causing a forward movement of the whole cell. This type of movement is so characteristic that the term **euglenoid movement** has been applied to it although it now appears that such movements occur only under unusual conditions. Active locomotion in *Euglena* is produced by a long whiplike structure, the **flagellum,** extending from the blunt end which, because it is the forward end in locomotion, is called the **anterior end.** The flagellum draws the euglena after it through the water by a lashing movement.

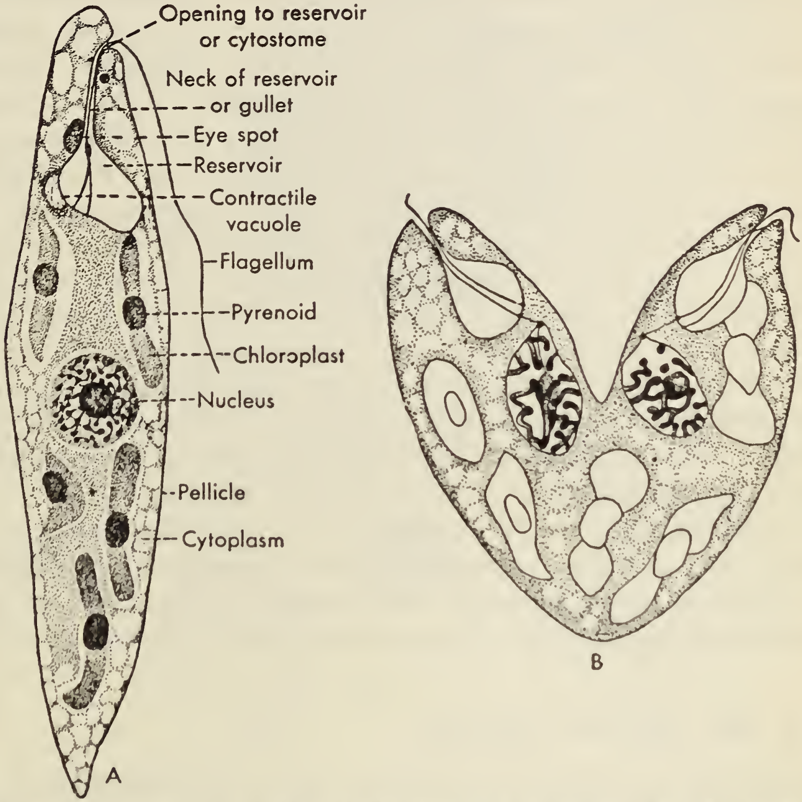


Fig. 18:7 *Euglena agilis.* On the left a free-swimming individual. On the right an individual in the process of division. After W. B. Baker, from MacDougall, *Biology, The Science of Life,* McGraw-Hill Book Company.

A small opening called the **mouth** in the anterior end leads into a short tube, the **gullet,** which in turn connects with a small round vesicle, the **reservoir.** Into the reservoir open **contractile vacuoles.** The flagellum is attached to the side of the gullet and passes out through the mouth. Near the attachment of the flagellum is a red **eyespot.** *Euglena* swims toward ordinary daylight but away from the direct rays of the sun. It has been shown experimentally that the eyespot is the part most sensitive to light. There is a single well-defined nucleus.

The cytoplasm of *Euglena* contains numerous chloroplasts. It is thus able, in the presence of light, to manufacture its own food materials from the carbon dioxide dissolved in the water, the water itself, and inorganic salts. *Euglena* probably never ingests materials by the so-called mouth. It has been shown that it can exist for a considerable time in the absence of sunlight if organic materials are in the water. Thus *Euglena* is able to obtain its food materials in two ways: by photosynthesis like a green plant or by absorbing organic food materials from its surroundings.

Euglena reproduces by **longitudinal division** (Fig. 18:7). The nucleus divides first. The cell division begins at the anterior end, the old flagellum going to one-half and a new one growing out from the other half. Under certain conditions the euglena may become spherical and form a gelatinous capsule or **cyst** around itself. It is then said to be **encysted.** In this condition the protoplast may divide. When conditions change the euglenas come out of the cyst and elongate.

On account of its chloroplasts *Euglena* is by many classified as a plant. Indeed, there is a large group of free-living flagellated organisms with this plantlike character which are therefore distinguished as phytoflagellates. Among them are many colonial forms. One of them is *Volvox.*

B. THE VOLVOX COLONY

Volvox has already been referred to under the Mastigophora. It is claimed by both botanists and zoologists. The botanists claim it because it manufactures its food by photosynthesis, the zoologists because its structure resembles that of a protozoan. It will now be described in some detail because its structure and life history illustrate some important biological principles. A full-grown colony of *Volvox* (Fig. 18:8) consists of several thousand individuals arranged to form a sphere. As they float in the fresh water of ponds and lakes the colonies appear as minute green balls varying in size up to 1 millimeter in diameter. Two kinds of individuals enter into the composition of a colony — vegetative individuals which are in the great majority and reproductive individuals. Both kinds of individuals are imbedded in a gelatinous matrix.

The **vegetative individuals** are typical flagellates. Each possesses two flagella which project outward from the colony, an eyespot or stigma, contractile vacuole, chloroplast, and nucleus. The vegetative individuals of the colony are in physiological communication with each other through strands of protoplasm passing through the gelatinous matrix. The movements of flagella cause the colony to rotate and move slowly through the water. The colonies are positively phototropic and tend to collect in the sunlight.

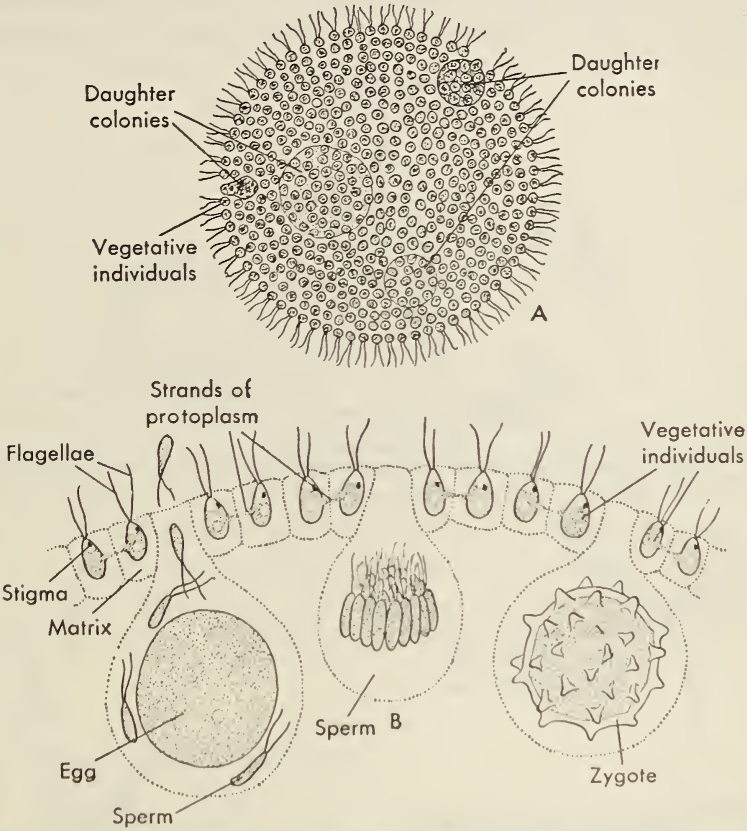


Fig. 18:8 *Volvox.* A, mature colony with daughter colonies produced from parthenogondia by asexual reproduction; B, details of vegetative individuals and sexual reproduction.

Young colonies consist entirely of individuals similar to the vegetative individuals. As a colony becomes mature reproductive individuals become differentiated. These are really reproductive cells of three kinds: **macrogametes** which develop into single, large, spherical eggs; **microgametes** which develop into numerous small flagellated sperms; and **parthenogonidia** which develop into colonies. The egg is fertilized in the colony and the zygote develops a resistant cell wall. In this condition it undergoes a period of rest and usually does not develop further until after the death of the colony. The parthenogonidia, as their name implies (Gr. *parthenos*, a virgin) resemble eggs but develop into colonies without fertilization. As is often the case among the lower organisms, sexual reproduction takes place in anticipation of a change in conditions while asexual reproduction, in this case by means of parthenogonidia, is a means of rapid multiplication when the conditions are favorable.

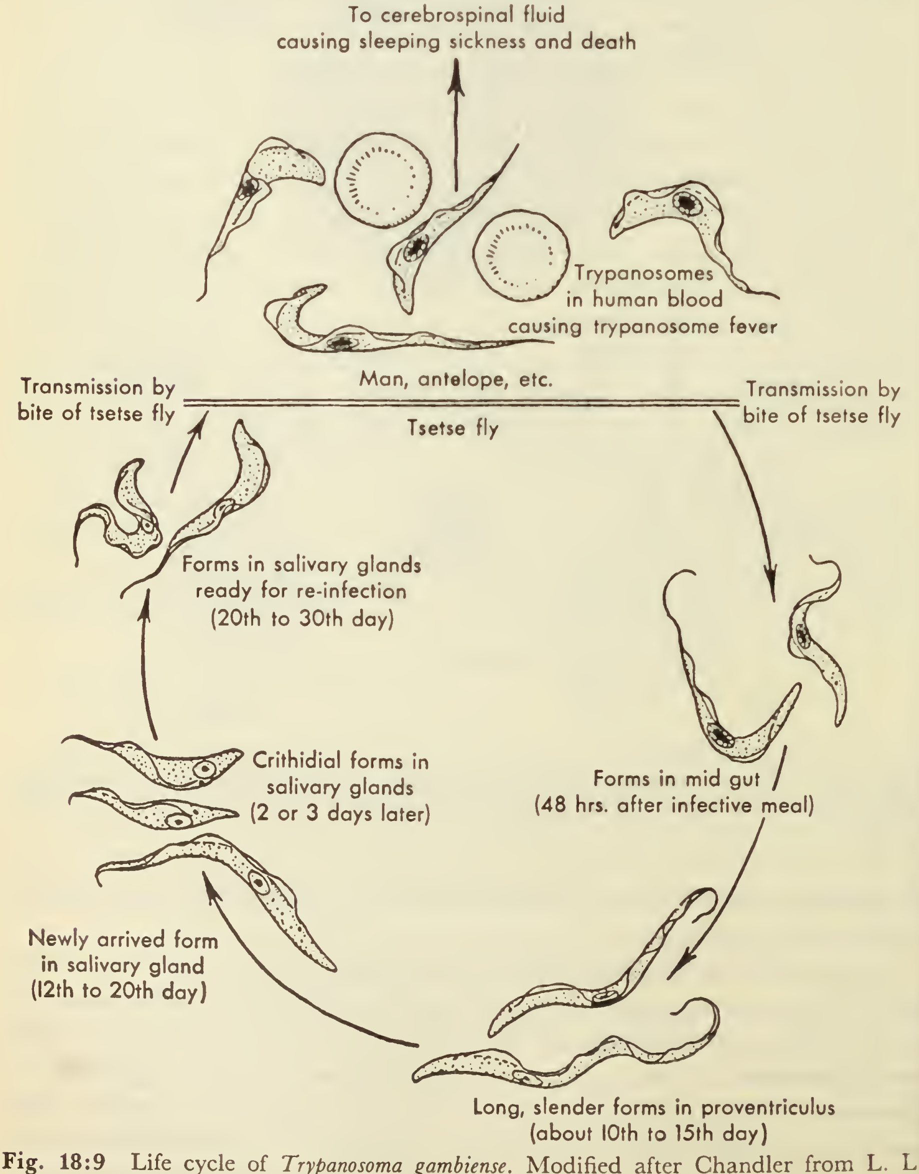

To cerebrospinal fluid causing sleeping sickness and death
Trypanosomes in human blood causing trypanosome fever
Transmission by bite of tsetse fly
Man, antelope, etc.
Transmission by bite of tsetse fly
Tsetse fly
Forms in salivary glands ready for re-infection (20th to 30th day)
Forms in mid gut (48 hrs. after infective meal)
Crithidial forms in salivary glands (2 or 3 days later)
Newly arrived form in salivary gland (12th to 20th day)
Long, slender forms in proventriculus (about 10th to 15th day)

Fig. 18:9 Life cycle of *Trypanosoma gambiense*. Modified after Chandler from L. L. Woodruff, *Foundations of Biology*, The Macmillan Company.

C. THE TRYPANOSOME OF SLEEPING SICKNESS

Many flagellates are parasitic; one of these is the deadly parasite of sleeping sickness, *Trypanosoma gambiense. Trypanosoma gambiense* lives in the blood of man and antelopes in central Africa, and in the intestine and salivary glands of a blood-sucking fly, the tsetse fly, by which it is transmitted from one mammalian host to another. The parasite of the blood is an elongated, cigar-shaped animal two or three times as long as the diameter of a human red corpuscle (Fig. 18:9). A single long flagellum arises near one end of the body and is attached to the body along nearly the whole of its length, forming an undulating membrane, the wavelike movement of which propels the trypanosome through the blood plasma. The trypanosomes multiply rapidly by fission in the blood. The "sleeping sickness" or coma occurs when the trypanosomes work their way into the nervous system. When an infected man or animal is bitten by a tsetse fly some of the trypanosomes are usually taken in with the blood into the fly's intestine. There the parasite passes through certain stages and after about three weeks is found in the salivary glands of the insect. Not until the trypanosomes have reached the salivary glands is the fly's bite infective. When this is the case the trypanosomes are injected into the blood with the saliva which the fly injects before sucking its meal. The injected trypanosomes are then ready to start the cycle again in their new host. The control of sleeping sickness depends upon the control or extermination of the tsetse fly in the particular region.

D. OTHER MASTIGOPHORA

The flagellated protozoa are a very large group. Besides the free-swimming and attached forms of fresh and salt water and the many parasitic forms in both invertebrates and vertebrates, there are a number of forms which occur in the soil where they seem to be of importance in causing the decay of vegetable matter.

3. THE CLASS INFUSORIA

The name "Infusoria" is given to these animals because they frequently occur in infusions. An **infusion** is formed when organic material is allowed to decay in water. The Infusoria occur abundantly in fresh water, in the sea, and as parasites in the intestinal tracts of other animals. The slipper animalcule, *Paramecium*, will be described as an example.

A. PARAMECIUM

Paramecium is a relatively elongated, single-celled animal which lives in stagnant water. One end, designated the anterior, since it is usually kept in advance, is rounded and flattened, while the other end, the posterior, is pointed. Since this general shape suggests a slipper, it is sometimes called the "slipper animalcule" (little animal). Like *Euglena* it has a thin outer covering or **pellicle,** and preserves a relatively fixed body shape. Extending from the flattened side of the anterior end, backward in the form of part of a long spiral to about the middle of the body, is a groove, the oral groove (Fig. 18:10). In place of the single flagellum, which forms the locomotor organ of *Euglena*, in *Paramecium* the entire surface of the body is covered with fine hairlike processes called **cilia.** The cilia beat the water in such a way as to make the animal move forward. The action of a cilium is somewhat similar to the stroke of an oar rowing a boat. During the forward part of its movement, however, the cilium is bent and offers less resistance to the water; during the backward part of its stroke it is straightened out and like an oar forces the paramecium along.

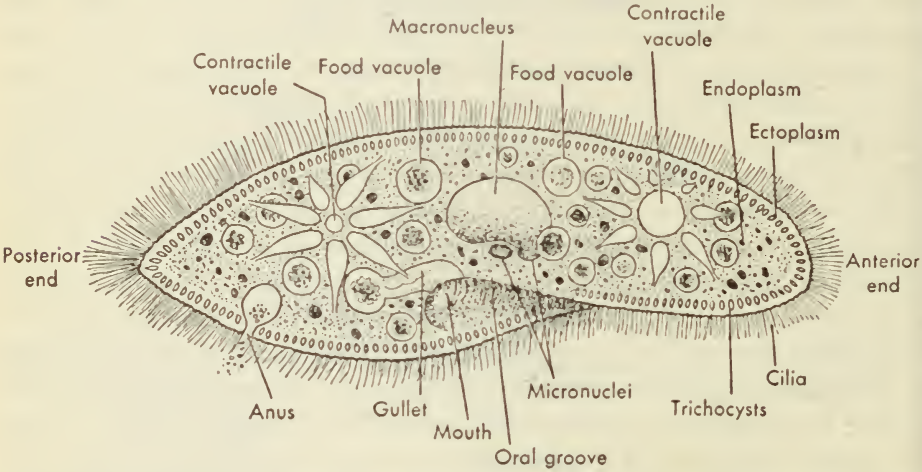


Fig. 18:10 *Paramecium*, showing internal structure. Somewhat diagrammatic. From Pfurtscheller wall chart, redrawn after Hegner, *College Zoology*, The Macmillan Company.

An outer layer of **ectoplasm** surrounding an inner granular **endoplasm** can be distinguished in the cytoplasm. In the ectoplasm just inside the pellicle are small spindle-shaped bodies called **trichocysts.** When the paramecium is irritated, the trichocysts explode, sending out long, fine threads into the surrounding water.

The oral groove is continuous through a **mouth** with a short tube, the

gullet. *Paramecium* feeds mostly on bacteria. These are driven by the movement of the cilia in the oral groove into the gullet, through which they pass. At the end of the gullet food vacuoles like those of amoeba are formed. In the **food vacuoles** digestion occurs, as in amoeba, and the nutrient material is absorbed. Due to a **cyclosis** similar to that which occurs in the elodea leaf the food vacuoles are moved along a course which carries them from one end to the other of the paramecium. After the nutritive material has been absorbed from a food vacuole the undigested material is expelled through a temporary opening called the **anus** which always re-forms at the same point on the surface of the body. At each end of the animal is a **contractile vacuole** into which run radial canals from the surrounding cytoplasm. The contractile vacuoles are lined by plasma membrane. Their function is probably the same as that of the contractile vacuole of amoeba. Oxygen is taken in through the plasma membrane over the entire surface of the body and through it also carbon dioxide and the excretory products are given off.

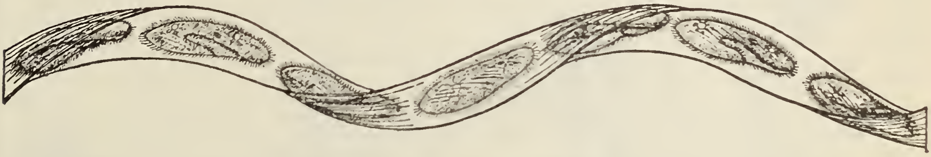


Fig. 18:11 *Paramecium caudatum.* Spiral path of a free-swimming specimen. The animal is moving from the left toward the right in the diagram. From Hegner, *College Zoology*, The Macmillan Company.

In traveling through the water paramecium follows a **spiral course.** The beat of the cilia is obliquely backward and across the body so that, while they force the animal forward, they also rotate it on its longitudinal axis. Also the cilia in the oral groove beat more vigorously than those over the rest of the body so that the paramecium tends to swerve toward the side of the oral groove. However, the rotation on the axis causes the animal as a whole to move in a spiral rather than a circle (Fig. 18:11).

One wonders how an animal as simple as paramecium is able to pick its way among the many obstacles in the pond and to find its food. Careful study has shown that on the whole the behavior of paramecium conforms to a few simple patterns. One of these is the **avoiding reaction.** When the animal encounters a solid object or an unfavorable, chemical environment in its path the cilia reverse their action and the animal moves backward for a short distance (Fig. 18:12). It then stops and the anterior end moves in a circle while water is driven into the oral groove. When the water sampled in the oral groove is suitable, forward movement is resumed in a new direction. If the object or chemical is reencountered the reaction is repeated, and will be repeated until a satisfactory course results. This type of reaction in which the animal seems to try and try again until it succeeds, has been called **trial and error.**

The nucleus of *Paramecium* may be considered as consisting of two distinct parts, a larger part called the **macronucleus,** and a smaller part, separated from this but lying close to it, called the **micronucleus.** The macronucleus seems to be concerned chiefly with the metabolism of the animal while the micronucleus is concerned with reproduction, especially sexual reproduction. Some species have two micronuclei.

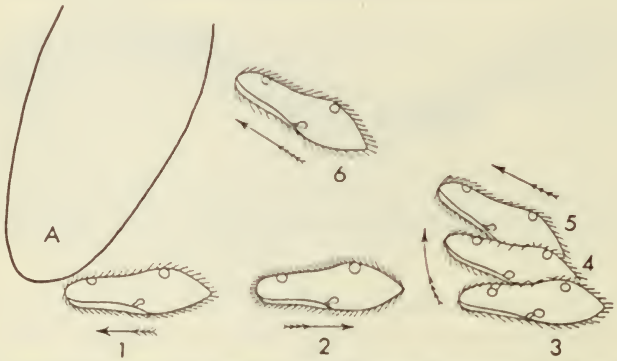


Fig. 18:12 *Paramecium caudatum.* Diagram of the avoiding reaction. A is a solid object or other source of stimulation. 1–6, successive positions occupied by the animal. The rotation on the long axis is not shown. After Jennings, from Hegner, *College Zoology*, The Macmillan Company.

Paramecium reproduces asexually by **transverse division** also referred to as fission (Fig. 18:13). Both the micronucleus and the macronucleus divide. This is followed by a constriction of the body in the middle region, the old gullet and oral groove going with the anterior half while a new gullet and oral groove are formed in the posterior half.

The usual means of reproduction of the Infusoria is by transverse division, in which process both the micronucleus and the macronucleus divide. However, at intervals a process called **conjugation** occurs which is usually followed by an increase in the rate of transverse division. When two paramecia enter into conjugation, they adhere by their ventral surfaces, at which point the cuticle and plasma membrane disappear, so that the protoplasm of the two individuals becomes confluent, forming a protoplasmic bridge. Now follows a series of nuclear changes in each of the two conjugants (Fig. 18:14). In each the micronucleus, which usually lies in a cavity of the macronucleus, moves out and becomes larger. It then forms a spindle and divides into two daughter nuclei.

Each of these then divides again into two giving four daughter micronuclei in each of the two conjugants. Three of the four micronuclei in each of the conjugants degenerate and the one which remains divides again, unequally however, one of the resulting daughter nuclei called the **female** being larger than the other which is called the **male.** The male micronuclei migrate across the protoplasmic bridge so that there results an interchange of male micronuclei between the two conjugants. In each conjugant the newly arrived male micronucleus fuses with the female micronucleus to form a **fusion nucleus,** the process being similar to the fusion of gametes to form a zygote. After this interchange of nuclei, the conjugants separate and are henceforth called **exconjugants.** Conjugation, which occurs not only in paramecium but generally in the Infusoria, is obviously to be explained as a **sexual process.** The male micronucleus, called also the **migratory nucleus,** is to be compared with the sperm nucleus of plants and animals, and the **stationary** female **nucleus** to the nucleus of the egg. The union of the two nuclei is really a process of fertilization. After the two conjugants separate, the macronucleus of each, which in the meantime has not divided, breaks up

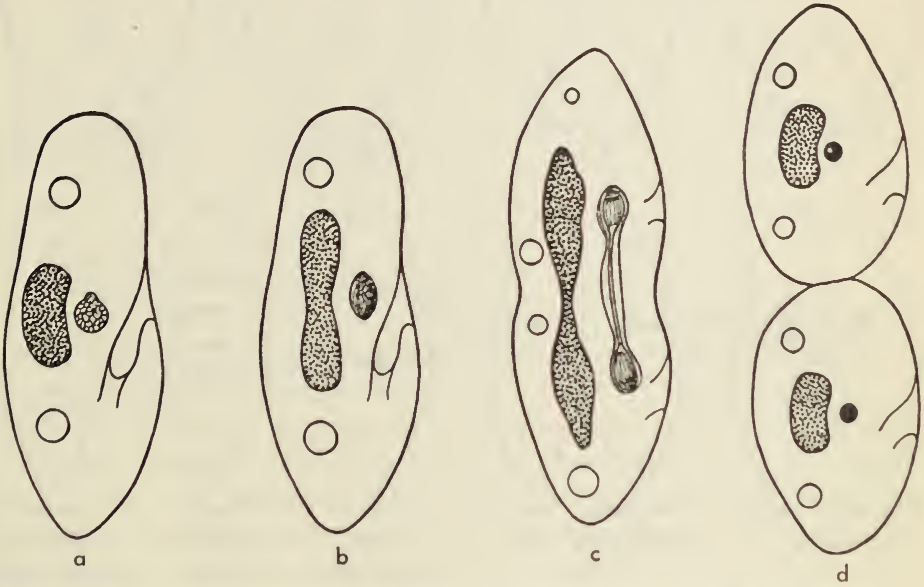
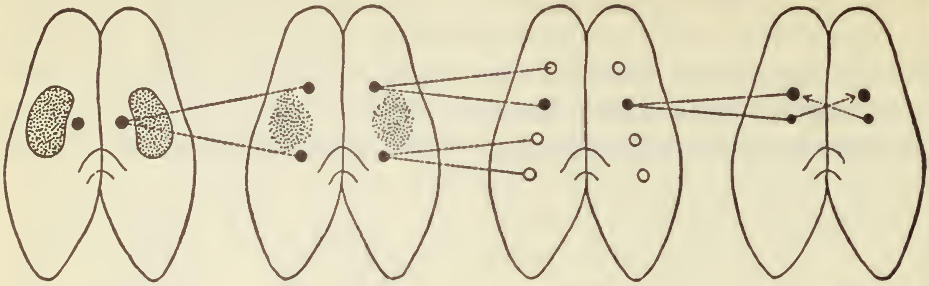


Fig. 18:13 *Paramecium caudatum.* Division: *a*, the micronucleus is beginning mitosis; *b*, the micronucleus is in mitosis and the macronucleus is beginning to elongate and constrict; *c*, the micronucleus is separating into daughter micronuclei and a second oral groove and two new contractile vacuoles have developed; *d*, the division is now complete and the daughter individuals are ready to separate. In the form of mitosis seen in the micronucleus the nuclear membrane remains intact. The macronucleus appears to divide by some form of amitosis. From Hegner, *College Zoology*, The Macmillan Company.

and degenerates. The fusion nucleus gives rise both to new macronuclei and to new micronuclei (Fig.18:14).

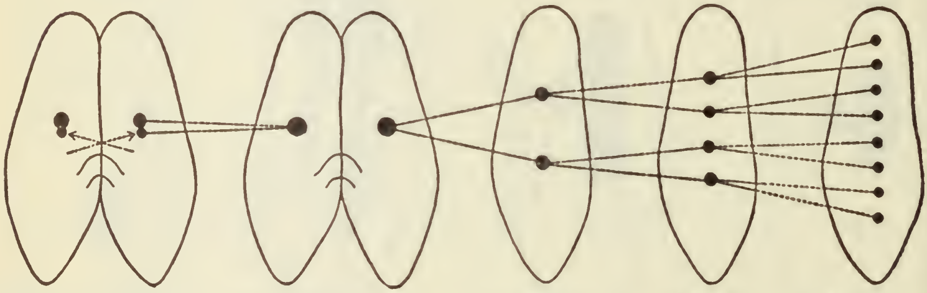


Conjugating pair

Micronuclei divide

Micronuclei divide again

Migratory and stationary nuclei



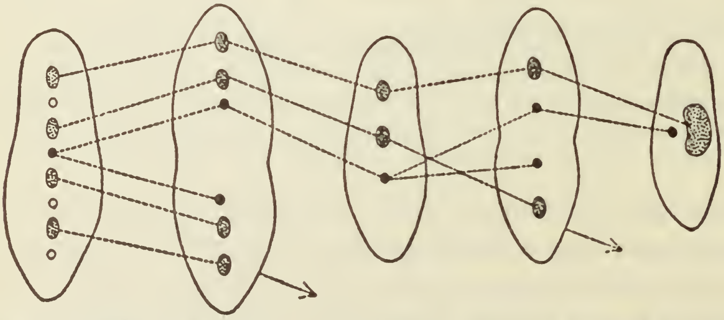
Migratory nuclei migrate

Migratory and stationary nuclei fuse

Fusion nucleus has divided

Nuclei divide again

Nuclei divide once more



Four micronuceli become macronuclei

Remaining micronucleus divides

Paramecium divides

Micronucleus divides again

Paramecium divides

Fig. 18:14 Diagrams illustrating the conjugation of *Paramecium caudatum*. After the fusion of the migratory and stationary nuclei the conjugating paramecia separate and proceed to divide transversely. Only one of each of the paramecia which result from each of these divisions is shown in each case in the diagrams. The micronuclei which degenerate are shown as small clear circles. Male nuclei are called migratory nuclei; female nuclei, stationary nuclei. Adapted from Hegner, *College Zoology*, The Macmillan Company.

Recent investigations have shown that not every individual will conjugate with every other individual. Thus in one species, *Paramecium bursaria*, three groups or physiological races have been distinguished and may be numbered I, II, and III. Individuals of group I will not conjugate with members of groups II and III nor will an individual of group II conjugate with one of group III. Nor does conjugation occur freely within the groups. In group I, for example, four mating types, designated A, B, C, and D, are distinguished such that individuals of type A will not conjugate with each other but will conjugate with members of type B, C, and D, and individuals of type B will not conjugate with each other but will conjugate with members of types A, C, and D. This condition does not appear to be one in which sex is involved but rather a condition in which the individuals from certain different groups or physiological races will not conjugate while individuals mating from the same group or physiological race but of different mating types will conjugate.

Since we have seen that conjugation is a sexual process, the question as to whether conjugation is really necessary in the life of the Infusoria is one of great interest. Will paramecium go on living and dividing by fission indefinitely if not allowed to conjugate? Conjugation can be prevented by isolating the individuals after each division. One investigator has done this with paramecium for over twenty years. During this time there were produced over twelve thousand generations (that is, fission occurred successively twelve thousand times) without conjugation. Conjugation, therefore, does not appear essential to the continued life of paramecium. In certain species and at certain times a phenomenon called **endomixis** appears to take the place of conjugation. In this process the macronucleus degenerates and the micronucleus divides giving rise to daughter nuclei, some of which become macronuclei and some form micronuclei, as occurs in the exconjugants subsequent to conjugation. The process takes place entirely within a single individual and there is no nuclear fusion.

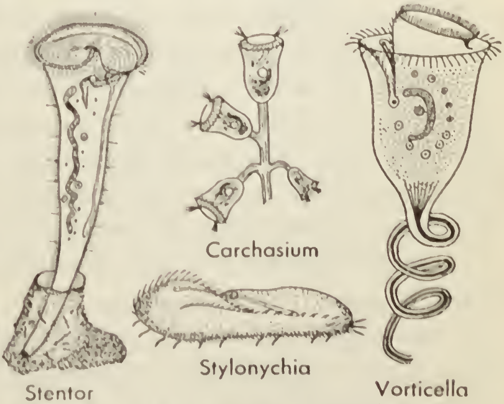


Fig. 18:15 Various types of infusoria.

B. OTHER INFUSORIA

Some of the Infusoria, such as *Vorticella*, live attached to aquatic plants or other objects by stalks, which may be either contractile or noncontractile. Some of the attached forms, such as *Carchesium*, form colonies. Other Infusoria are parasitic either on the surface of other animals, like the little disc-shaped *Trichodina* which creeps over *Hydra*, or in the interior of animals, especially in the intestines of vertebrates, like *Balantidium coli* which occurs in man, and *Opalina* which occurs in the frog (Fig.18:15).

4. THE CLASS SPOROZOA

The Sporozoa are all parasitic in the bodies of other animals. The name "Sporozoa" is applied to them because they usually produce spores. The formation of spores is usually associated with the transfer of the parasite from host to host. There are many different kinds of Sporozoa and almost every phylum of the animal kingdom includes at least some hosts of these parasites.

A. THE MALARIA PARASITE

The most famous of all the Sporozoa is the organism which causes malarial fever. This organism, called *Plasmodium*, is found in the red corpuscles of the blood of persons suffering from malaria (Fig. 18:16). There are three common kinds of malaria, which are recognized by the number of days intervening between the recurring fevers. Tertian malaria, in which the fever occurs every third day, is caused by *Plasmodium vivax*. The malarial parasite occurs in the red corpuscle as a small amoeboid **trophozoite.** This increases in size until it almost fills the corpuscle. There then follows repeated division of the nucleus followed by a division of the cytoplasm of the parasite to form small cells called **merozoites.** These are liberated into the plasma of the blood and attack new red blood corpuscles. Here the merozoites become trophozoites, increase in size, and form a second generation of merozoites. The cycle from merozoite to merozoite takes 48 hours. Tertian malaria is characterized by an attack of fever every 48 hours. Examination of the blood shows that the onset of the fever occurs shortly after the merozoites are liberated into the blood. Presumably the liberation of the merozoites into the blood is accompanied by the liberation of some poison.

As the disease progresses and the parasites become abundant in the blood, other stages leading to sexual reproduction are found. These are the **male gametocytes** and the **female gametocytes.** The gametocytes do not develop further in the human host. Only when the diseased person is bitten by a female mosquito of the genus *Anopheles* and the latter sucks them into its digestive tract with its meal of human blood, can the gametocytes continue their development. In the stomach of the mosquito the female gametocytes become transformed by a process referred to as maturation into female gametes or **ova** and the male gametocytes throw off numerous slender microgametes or **spermatozoa.** Fertilization occurs in the stomach of the mosquito. The zygote, called an **ookinete,** enters the lining of the stomach of the mosquito and forms an **oocyst** in the stomach wall. In this cyst, by repeated division, a large number of **sporoblasts** are formed. Each sporoblast, while still in the cyst, forms numerous slender **sporozoites.** The sporozoites become liberated into the blood of the mosquito and are carried to the salivary glands. From the salivary glands of the mosquito, the sporozoites are

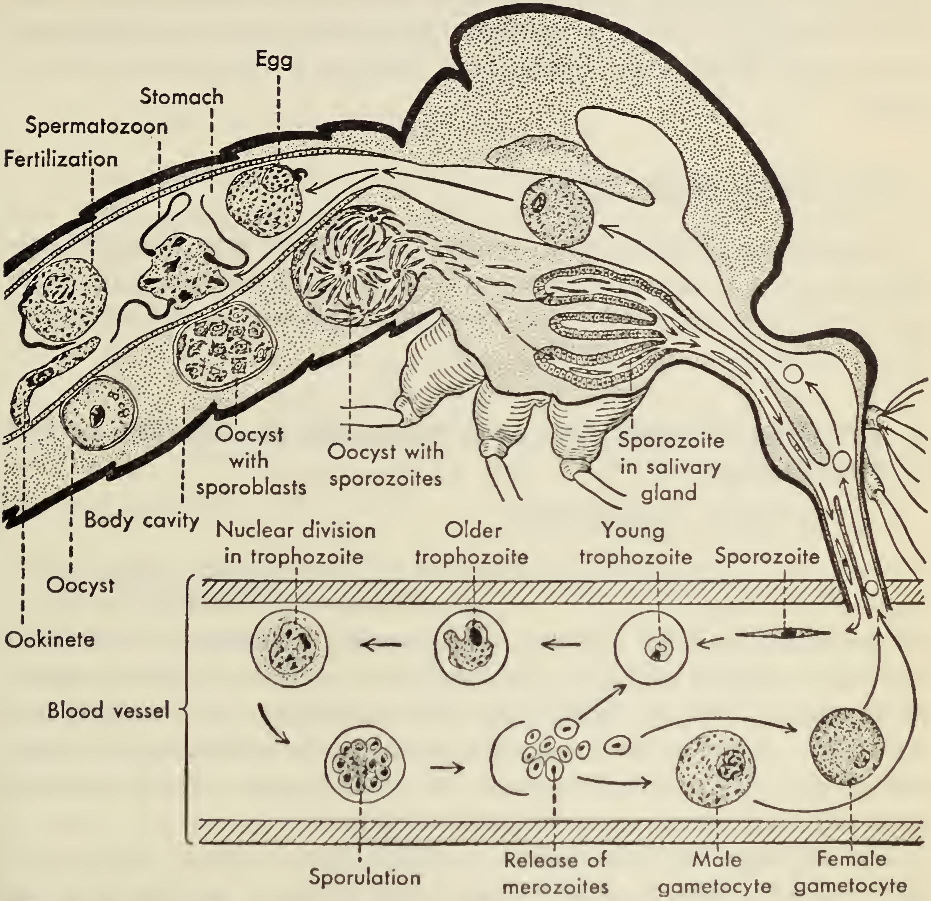


Fig. 18:16 *Plasmodium vivax,* the cause of tertian malaria. Diagram of a section of a mosquito's body (above) and of a section of a human blood vessel (below) to show the life cycle. The zygote formed by the fertilization of the egg by a spermatozoon becomes a motile ookinete which penetrates the wall of the intestine of the mosquito and there becomes an oocyst. From Hegner, *College Zoology,* The Macmillan Company.

injected into the human host by the mosquito when it bites. The sporozoites attack the red corpuscles and become trophozoites ready to cause the disease.

Probably more people have died from malaria than from any other single human disease. The method of prevention is now clear — the destruction of the mosquito, *Anopheles*. Quinine kills the malarial parasites while in the blood of the patient and therefore is an effective curative agent.

B. OTHER SPOROZOA

A sporozoan (*Monocystis*) of a somewhat different type from the malarial parasite occurs rather frequently in the reproductive organs (seminal vesicles) of the earthworm. Another (*Gregarina*) occurs commonly in the cockroach.

5. BIOLOGICAL PRINCIPLES AND PROBLEMS ILLUSTRATED IN THE PROTOZOA

A. COLONY FORMATION

A colony is a group of individuals of the same species which live together, but nevertheless carry on independently their ordinary metabolic functions. Is the volvox a colony of single-celled individuals or is it an individual composed of many cells? Since the vegetative cells are capable of carrying on independently their own metabolism and are alike and not differentiated to perform special functions the volvox may be properly considered a colonial organism. We shall later encounter numerous cases of colony formation in multicellular animals.

The volvox colony illustrates a possible step in the evolution of a multicellular organism. Indeed, were the vegetative individuals of the volvox colony not all alike and some of them were differentiated from the others to perform special functions, we would already have a multicellular individual and not a colony. We shall have to refer to volvox in our subsequent study of certain animal types and in our discussion of the evolution of animals.

B. BODY CELLS AND GERM CELLS

We will see later that a sharp distinction can be made in nearly all multicellular animals between the cells which make up their bodies, called **somatic cells,** and the cells which are concerned in the reproduction of the species, called **germ cells.** The somatic cells die when the individual dies, the germ cells live on from generation to generation. In the differentiation of the cells of the volvox colony into vegetative cells and reproductive cells, we see what may be regarded as a step toward the division of the bodies of multicellular animals into somatic cells and germ cells.

C. DEATH IN THE PROTOZOA

Do protozoan individuals die of old age? When an amoeba, a euglena, or a paramecium reaches a certain size, it simply divides, forming two new individuals. If it dies it is because of adverse conditions in its environment (e.g., enemies, lack of nourishment, and so on) or diseases caused by parasites. There seems to be no question of death from old age. Only when there is a differentiation into vegetative individuals and reproductive individuals as in the volvox colony do we find certain individuals, the vegetative individuals, incapable of reproducing or continuing their existence beyond that of the colony, and therefore doomed to a limited span of life.

D. PARASITISM

We have found that parasitic species occur in all of the four classes of Protozoa and that one whole class, the Sporozoa, consists entirely of parasitic species. In some cases the parasite is able to pass through its whole life cycle in one host. In other cases, as in the case of the human diseases African sleeping sickness (trypanosomiasis) and malaria, the parasite requires for its complete life cycle two hosts. The use of an intermediate host such as the tsetse fly or mosquito makes possible a wide and rapid spread of the parasite but at the same time offers a certain means of prevention in the destruction of this intermediate host. Certain parasites, like *Endamoeba coli*, seem to be practically harmless, while others resembling them, like *Endamoeba histolytica*, are often fatal. We will later encounter numerous cases of multicellular parasites which present essentially the same problems as do protozoan parasites.

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1. The class Sarcodina 369
    A. *Amoeba*, a unicellular animal 369
    B. Other Sarcodina 373

2. The class Mastigophora 374
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5. Biological principles and problems illustrated in the Protozoa 388
   - A. Colony formation 388
   - B. Body cells and germ cells 388
   - C. Death in the Protozoa 389
   - D. Parasitism 389

Questions

1. Give the names and characteristics of the four classes of Protozoa. What features of the organisms are taken as the basis of the division into classes?
2. Of what importance are the Foraminifera and Radiolaria in the economy of nature?
3. Describe the life history of *Trypanosoma gambiense*. What disease does it cause? How may the disease be prevented?
4. Describe the process of conjugation in *Paramecium*.
5. Why is conjugation to be considered a sexual process?
6. Is conjugation necessary? What may take its place?
7. Describe the life cycle of *Plasmodium vivax*. What are the advantages to the parasite in having two hosts? What are the disadvantages?
8. Outline the life history of *Volvox*.
9. Discuss the question whether *Volvox* is a colonial organism.
10. How do somatic cells differ from germ cells?
11. Does death from old age occur in the Protozoa?
12. Make a list of all the protozoan parasites referred to in this chapter for which man may be a host. In what parts of the world do they occur?

Suggestions for Further Reading

Calkins, Gary N., *The Smallest Living Things*, The University Society, New York, 1935.

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Chandler, Asa C., *Introduction to Human Parasitology*, Part I, "The Protozoa," John Wiley & Sons, Inc., New York, 1930.

CHAPTER 19

Saclike Animals with Ectoderm and Endoderm (Phylum Coelenterata)

The term **Metazoa** is used to include all animals other than the Protozoa, in other words all the animals in which the individual consists of more than a single cell. The Metazoa include many phyla, indeed all those of the animal kingdom except the Protozoa. It will not be possible in this text to consider in detail all the phyla. Those phyla have therefore been selected for study which illustrate best the more important problems and principles of biology. We begin our study of the Metazoa with the phylum Coelenterata. The characteristics of the Coelenterata were discussed in Chap. 3, and an animal belonging to the phylum, the fresh-water hydra, was described in Chap. 2.

A characteristic feature of the Coelenterata which was not thought to be of sufficient general interest to be included in the description of *Hydra*, is the possession of stinging cells, called **cnidoblasts** (Gr. *knide*, nettle + *blastos*, here a cell). Indeed, so conspicuous a feature is this of the Coelenterata that at one time it gave its name to the group which was then called Cnidaria.

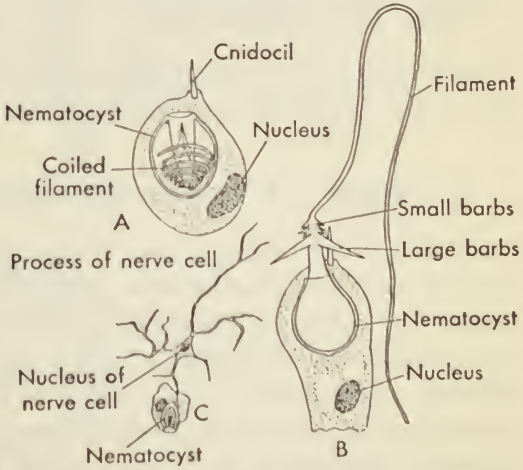

Fig. 19:1 *Hydra*, nematocysts. A, a nematocyst contained in its cnidoblast; B, the same after extrusion of the thread; C, a cnidoblast, with which a nerve cell is associated. Redrawn after Parker, after Schneider.

The cnidoblasts occur in the epidermis and often project somewhat from the general surface of the body. They are usually most abundant in the tentacles. Each cnidoblast contains a small bladderlike structure called a **nematocyst** (Gr. *nema*, *nematus*, a thread + *kustis*, a bladder) which contains a long, fine, coiled thread (Fig. 19:1). Projecting into the water from the outer surface of each cnidoblast is a pointed protoplasmic process called a **cnidocil.** When a cnidoblast is stimulated, its protoplasm contracts, squeezing the nematocyst and forcing the coiled thread, which it contains, out into the water. When this happens, a number of barbs appear, extending from the thread near where it is attached to the nematocyst. The stimulation of the cnidoblast appears to be partly a matter of the presence of food substances in solution in the surrounding water, which seem to sensitize the cell, and mechanical stimulation of the cnidocil. The nematocysts are used by hydra in catching its prey, and to some extent as a protection against attack by other animals. In some cases the threads, when extruded, twine around the small animal or plant and hamper its movement. In other cases the threads apparently inject some poisonous substance which paralyzes the prey. The phylum Coelenterata is divided into three classes, the Hydrozoa, Scyphozoa, and Anthozoa.

1. TYPES OF HYDROZOA

Hydra (Fig. 19:1), already described in Chap. 2, is a member of this class. More typical of the class is *Obelia.*

A. OBELIA — *A COLONIAL HYDROID*

Obelia is a colonial organism found in the sea (Fig. 19:2). It consists of numerous individuals called **polyps,** not unlike individuals of *Hydra.* Indeed one can form a fairly good picture of the general structure of an obelia colony by imagining a hydra to which the buds have remained attached. An obelia colony consists of a **stem** from which many short branches arise and bear at their tips the polyps. The cells of the stem and branches constitute a living connection between the polyps, called the **coenosarc.** The coenosarc is composed of epidermis and gastrodermis which are continuous with the epidermis and gastrodermis of the polyps and contains a gastrovascular cavity which is continuous with the gastrovascular cavities of the individual polyps. Surrounding the stem and its branches and forming cups into which the polyps can retract is the **perisarc,** composed of a substance secreted by the epidermis.

The polyps of the *Obelia* colony are of two kinds. The **vegetative polyps** borne on the ends of the branches have numerous tentacles in a circle around the mouth. When the polyp is expanded the mouth is funnel-shaped. The **reproductive polyps,** which are borne in the angles between the branches and the main stem, are without a mouth or tentacles, obtaining their nourishment, like the coenosarc, from the food taken in by the vegetative polyps. Around the vegetative polyps the perisarc takes the form of **hydrothecae** (Gr. *hydra* + *theca*, a box) and around the reproductive polyps it takes the form of **gonothecae** (Gr. *gonos*, reproduction).

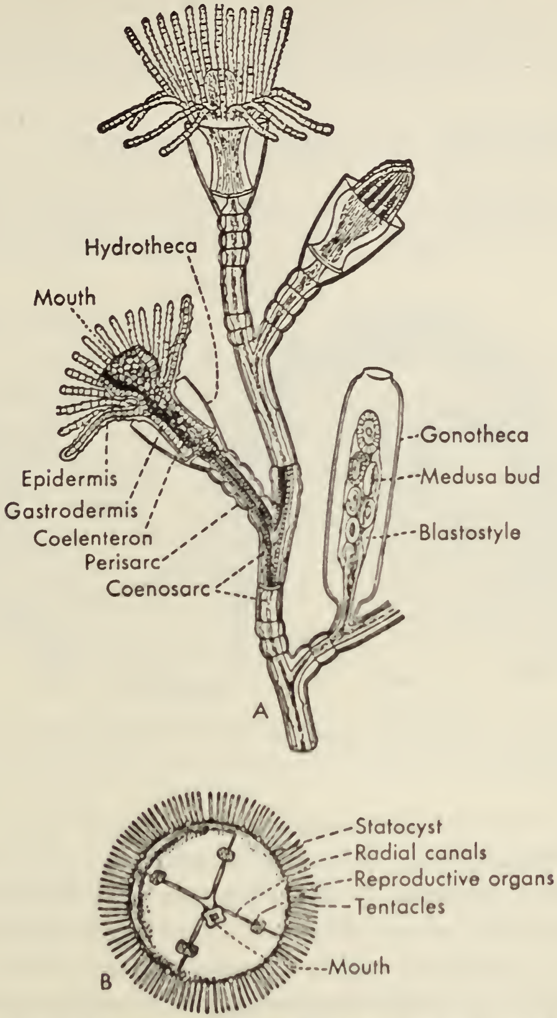

Fig. 19:2 *Obelia.* A, colony bearing vegetative and reproductive individuals; B, a medusa, view of the under or oral side. A and B are not of the same species. After Parker and Haswell, from Hegner, *College Zoology*, The Macmillan Company.

The obelia colony reproduces asexually by the budding of the reproductive polyps. The buds grow into small, free-swimming individuals, resembling jellyfish and called **medusae.** The medusae are sexual individuals, some producing sperm and others eggs. The zygotes resulting from the fertilization of the eggs develop into larvae which are at first free-swimming, but later become attached and develop into new colonies. In place of describing a medusa of *Obelia*, we will describe a better known and more easily obtained medusa, of the genus *Gonionemus.*

B. GONIONEMUS — *A HYDROID MEDUSA*

This little medusa or jellyfish is common in shallow water along the eastern coast of the United States (Fig. 19:3). It measures from 1 to 2 centimeters in diameter when mature. The general shape of the animal is like that of an umbrella. It is usually oriented in the water with the convex surface uppermost. From what corresponds to the rim of the umbrella extend numerous **tentacles.** The handle of the umbrella is represented by a structure called the **manubrium.** At the lower end of the manubrium is the **mouth opening.** The upper convex surface is called the **exumbrella,** the concave surface from which the manubrium projects, the **subumbrella.**

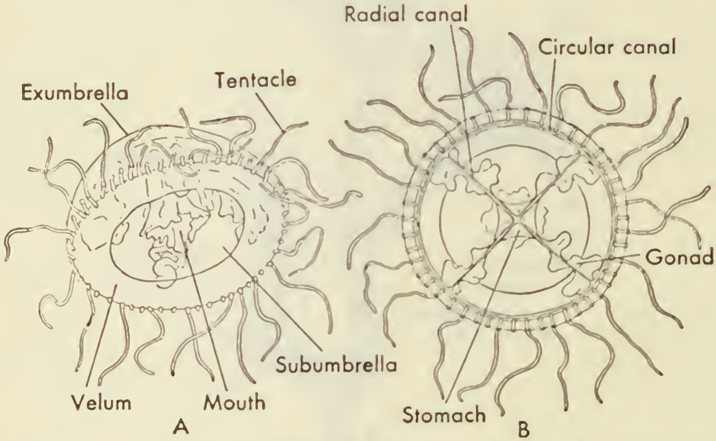

Fig. 19:3 *Gonionemus*, a hydrozoan medusa. A, viewed from the under side; B, viewed through the upper side.

It is instructive to compare the general structure of the medusa with that of the polyp (Fig. 19:4). To do this, we must imagine the polyp inverted and turned with the hypostome and mouth down. The gastrovascular cavity of the medusa is very much reduced. The central cavity into which the mouth opens is continued into four radial canals which connect with a circular canal running around the outer rim to which the tentacles are attached. The exumbrellar and the subumbrellar surfaces are covered with epidermis. The gastrovascular cavity is lined with gastrodermis. Between these two layers is the mass of mesoglea or jelly which gives to the animal the name of "jellyfish."

A membrane called the **velum** formed of epidermis and including a thin layer of mesoglea projects from the inner portion of the rim, partly enclosing the subumbrellar space. The nerve net is especially developed in the region of attachment of the velum, forming a **nerve ring.** Between the bases of the tentacles are small sense organs called **statocysts** which enable the medusa to orient itself to the pull of gravity. The medusa swims by taking water in through the opening in the velum and expelling it again by a violent contraction of the body.

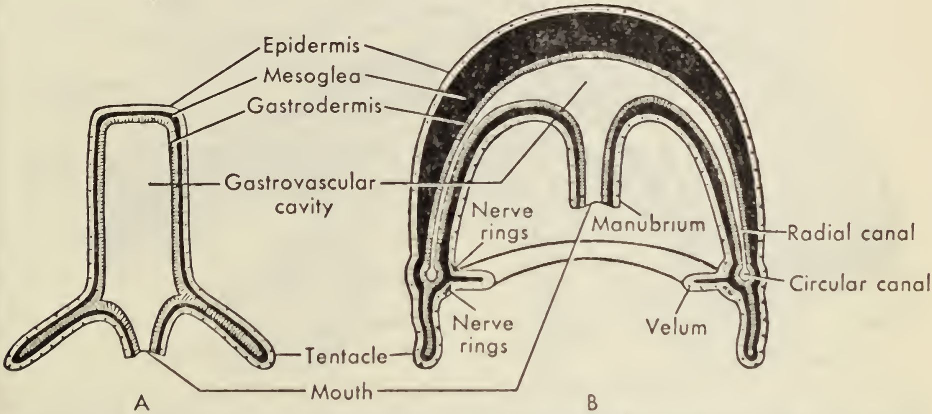

Fig. 19:4 Diagrams comparing the structure of a polyp (A) and a medusa (B). Gastrovascular cavity is synonymous with coelenteron. After Parker, from L. L. Woodruff, *Animal Biology*, The Macmillan Company.

In *Gonionemus* the sexes are separate. The **testes** or **ovaries** appear as four ruffled, pinkish bodies arranged one on each radial canal. The eggs and sperm are discharged directly into the water and fertilization takes place there.

Although most medusa are marine, of recent years some fresh-water species have been found to occur rather commonly.

C. PHYSALIA — A *POLYMORPHIC HYDROZOAN*

One of the most interesting and beautiful of Coelenterates is another colonial form, the Portuguese man-of-war, *Physalia.* The colonies of *Physalia* float on the surface of the ocean by means of a large float with a saillike crest. From this the polyps hang down suspended in the water. These colonies contain a number of different kinds of individuals and are therefore said to be **polymorphic.** Some of the polyps are nutritive; some are protective and contain batteries of nematocysts; some are for locomotion, lacking tentacles and a mouth; some are reproductive and produce medusae; while still others are of unknown function.

2. THE JELLYFISH, *AURELIA,* A TYPE OF SCYPHOZOA

One of our commonest large jellyfishes, all of which are marine, is *Aurelia* (Fig. 19:5). Apart from its larger size, *Aurelia* differs from *Gonionemus* in being without a velum, in the position and shape of its gonads, the arrangement and structure of its sense organs, and in having a more complicated canal system. In general shape and appearance, *Aurelia* is not unlike *Gonionemus.* While, however, *Gonionemus* rarely exceeds 2 centimeters or 4/5 inch in diameter, *Aurelia* often reaches a diameter of 30 centimeters (1 foot) or more.

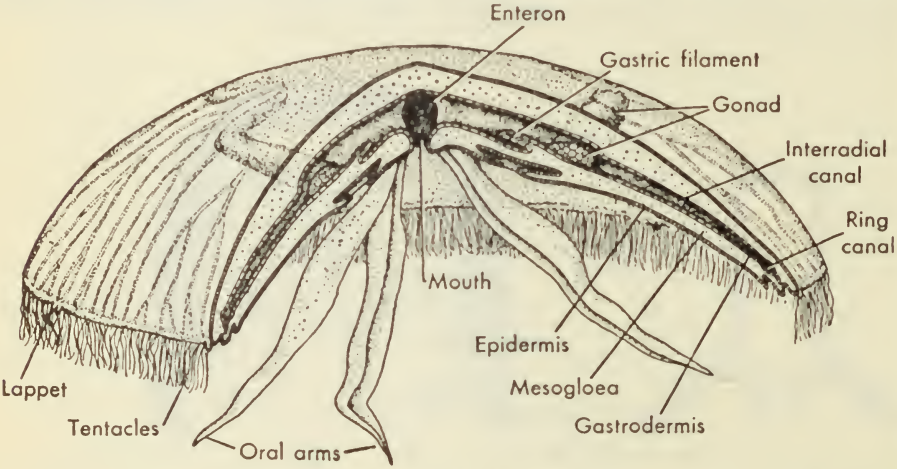

Fig. 19:5 *Aurelia,* a large scyphozoan jellyfish. In the diagram one quarter of the body has been cut away to show the internal structure. From Storer, *General Zoology*, McGraw-Hill Book Company, Inc.

As in *Gonionemus* there are **exumbrellar** and **subumbrellar** surfaces, and extending from the latter a manubrium at the free end of which is the **mouth.** In the region of the mouth the **manubrium** is expanded in its lower portion into four **oral arms** which extend out from the four corners of the square-shaped **mouth.** The outer epidermis extends inward from the mouth forming a short **gullet.** This leads to an **enteron** lined with gastrodermis from each of the sides of which a **gastric pouch** extends laterally. From the gastric pouches lead numerous **radial canals** which branch repeatedly and join with a **ring canal.** In the gastric pouches are **gastric filaments** bearing **nematocysts.** The sense organs of

Aurelia are somewhat more highly developed than those of *Gonionemus.* Eight notches spaced at equal distances in the margin of the umbrella lodge these sense organs, each consisting of a **statocyst** and an **eyespot.** Bordering the notches are small projections known as **lappets.**

The gonads are developed in the walls of the gastric pouches. When ripe the eggs or sperm are discharged into the gastric pouches and from there pass through the stomach and gullet to the outside. The fertilized eggs develop into hydralike individuals which reproduce by budding. Later, medusae are formed by a peculiar process called **strobilization** in which a hydralike individual divides transversely beginning at the oral end and forms a succession of saucer-shaped bodies, each of which develops into a medusa (Fig. 19:6).

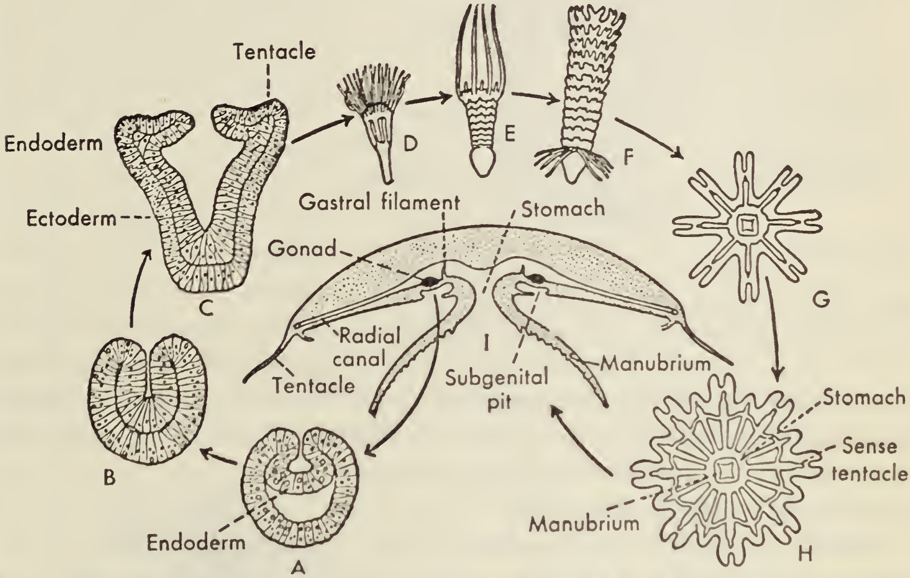

Fig. 19:6 The life cycle of a scyphozoan medusa, Aurelia. A, B, C, longitudinal sections through early stages in the development of the zygote; D, E, F, the formation of young medusae by strobilization; G, H, young medusae; I, a vertical section through an adult medusa. From Hegner, *College Zoology*, The Macmillan Company.

3. A SEA ANEMONE, A TYPE OF THE ANTHOZOA

The sea anemones are common on all coasts attached to rocks and wharves and in tide pools (Fig. 19:7). In shape an anemone is not unlike a hydra. Many species are, however, much larger, reaching a diameter of from 3 to 6 centimeters. The tentacles are usually very numerous and are arranged in a number of circles. The epidermis is turned in at the mouth forming a **gullet** as in *Aurelia.* Two ciliated grooves or **siphonoglyphs** extend down the gullet and serve to carry food into the gastrovascular cavity. Extending from the gullet in the gastrovascular cavity to the body wall are numerous membranous **mesenteries,** radially arranged. Below the gullet the edges of the mesenteries carry fine threadlike **acontia** which contain nematocysts. The acontia may be thrust out through minute pores in the body wall.

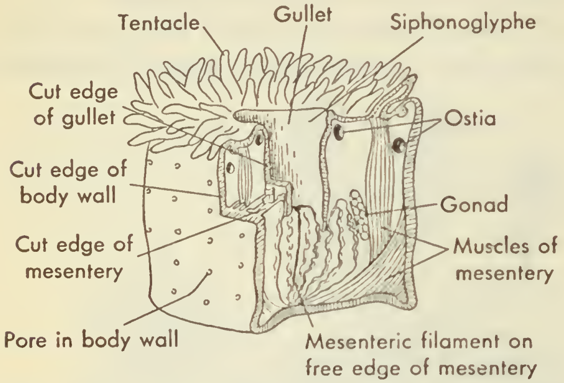

Fig. 19:7 A dissection of a sea anemone (*Taelia crassicornis*). Redrawn after Parker and Haswell.

The sexes are separate and the **gonads** are developed in the mesenteries. The ripe eggs or sperm are shed into the gastrovascular cavity and pass out by the mouth. The fertilized egg develops into a small, ciliated, pear-shaped **planula,** which after swimming about for a short time becomes attached and develops into a polyp such as that already described.

Corals are similar in structure to sea anemones and differ from them chiefly in forming skeletons and colonies. They are in part responsible for the Great Barrier Reef of Australia and for the coral islands and atolls of the tropical and semitropical parts of the Pacific and Atlantic oceans. Corals occur abundantly as fossils and there is a long record in the rocks of their occurrence in the sea. The red or pink coral (Fig. 19:8) used for necklaces and other ornaments is obtained by dredging in the southern Mediterranean and off the Cape Verde Islands. Cheaper varieties are obtained from Japan and Australia. Coral varies greatly in value, depending especially on the color. The finest shades may sell for as much as $600 per ounce, while little pieces of inferior quality may bring only $1.00 an ounce. Corals are of indirect economic value in forming coral reefs and islands.

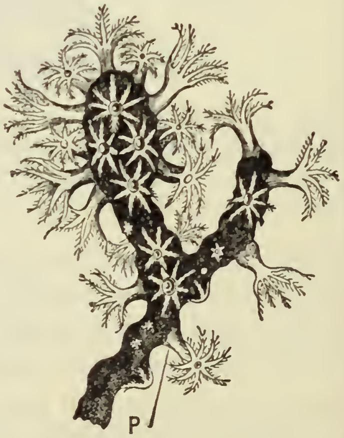

Fig. 19:8 A branch of a precious coral (Corallium rubrum). P, a living polyp expanded. From Sedgwick, *A Textbook of Zoology*, Swan Sonnenshein & Co. Ltd.

4. BIOLOGICAL PRINCIPLES AND PROBLEMS ILLUSTRATED IN THE COELENTERATA

A. THE SACLIKE TYPE OF STRUCTURE

The coelenterate individual consists of a sac in which a cavity, the gastrovascular cavity, is enclosed by two layers of cells, the epidermis which is on the outside and the gastrodermis which lines the cavity. This saclike type of structure seems to be a fundamental one in the animal kingdom. Most animals which show a more complicated structure than the Coelenterata go through a stage in their early development, called the **gastrula,** which resembles *Hydra* in being saclike and in containing a cavity, called in this case the **archenteron,** surrounded by two layers of cells, called in this case the **ectoderm** and **endoderm.**

The outer or epidermal layer of the coelenterates is clearly seen to be protective and to form that part of the animal which is most intimately in contact with the outside world. The inner layer, or gastrodermis, is chiefly concerned with digestion and absorption of food. This division of labor between the epidermis and gastrodermis occurs also in the animals more highly organized than *Hydra* in that those parts of their bodies which are protective and concerned with the maintenance of the animal's contact with the external world (e.g., nervous system) are developed from the ectoderm, while those structures which are concerned with the digestion and absorption of food (e.g., lining of the digestive system) are developed from the endoderm. Organisms in which the only cell layers present are developed from ectoderm and endoderm are said to be **diploblastic** (Gr. *diploos*, double + *blastos*, a sprout, in combinations usually an embryonic tissue or layer). Coelenterates are diploblastic animals.

Thus *Hydra* and the Coelenterata in general are interesting, not only because they are animals built on what is perhaps the simplest multicellular plan found in the animal kingdom, but also because they closely resemble, in their adult condition, a fundamental stage in the development of most animals of more complicated structure.

B. DIFFERENTIATION

With the development of a multicellular body and the arrangement of the cells in two layers differing in the role which they play in the economy of the animal, comes also cell differentiation. The epidermis of hydra contains cnidoblasts, epidermal cells, nerve cells, and interstitial cells differing markedly in structure and the part they take in the life of the animal, although all are more or less concerned in its relations with its environment. The gastrodermis, on the other hand, contains gland cells, absorbing cells, nerve cells, and interstitial cells, which also differ among themselves although concerned in general with the work of digesting, ingesting, and distributing food. Certain parts of the body are differentiated to form organs with special functions. Thus the tentacles are sense organs, and organs for food getting and protection. The ovaries and testes are reproductive organs.

C. ALTERNATION OF GENERATIONS

The Coelenterata provide some of the best examples in the animal kingdom of an alternation of generations. As already explained in the case of plants, by an alternation of generations is meant the alternation of a generation which reproduces only asexually with the one which reproduces sexually. In the coelenterates, where there is an alternation of generations, the medusa stage represents the sexual stage while the polyp stage represents the asexual generation. In *Hydra* there is no alternation of generations, both sexual and asexual reproduction occurring in the polyp stage. In *Obelia*, on the other hand, there is a typical alternation of generations, the colony representing the asexual generation and the medusa the sexual generation. In some species of Hydrozoa, the polyp stage is absent, the medusa stage giving rise directly to medusae. In *Physalia*, an alternation of generations can be identified but the sexual (medusa) stage is small and of short duration. Just the reverse is true in the case of *Aurelia* where the large and conspicuous stage is the medusa (sexual) and the asexual stage (strobila) is reduced. In the sea anemones and in the corals there is no medusa stage and no alternation of generations.

There is a fundamental difference between the alternation of generations which occurs in plants and that which occurs in coelenterates. This has led to the use of the term **metagenesis** (Gr. *meta*, after + *genesis*, generation) in the case of the life cycle of the coelenterates. In plants, as already described, the sporophyte stage or generation which reproduces asexually has cells with diploid nuclei, while the gametophyte generation which forms gametes and reproduces sexually has haploid nuclei, the reduction from the diploid to the haploid number of chromosomes occurring during spore formation or just previous to the asexual reproduction. In coelenterates, on the other hand, when an alternation of generations occurs the individuals of both generations have the diploid number of chromosomes and reduction occurs during the formation of the gametes in the sexually reproducing individual, that is, the medusa or jellyfish. Nevertheless, the alternation of generations has the same effect in each case: asexual reproduction leads to a wider distribution of the species through the formation of spores which are scattered by the wind in one case and in the other through the formation of medusae or jellyfish which are carried about by water currents; while sexual reproduction leads in each case to the production of new individuals through the fusion of gametes.

D. COLONY FORMATION

Colonies of individuals are commonly formed in the Hydrozoa and the Anthozoa. These colonies are formed by repeated budding or fission from a single original individual. This type of colony differs in many respects from the colonies of insects, which are more properly referred to as societies, and which are discussed in Chap. 24. In a colony there is usually a division of labor among the individuals. This is generally accompanied by a structural differentiation of the individuals, so that some are specially adapted to perform one or more functions for the colony, while others perform other functions. This differentiation into individuals of different types is called **polymorphism.** It is well illustrated in *Physalia.*

E. SYMBIOSIS

Hydra is not the only coelenterate which harbors symbiotic algae in its endoderm. Many of the Anthozoa also do so. An interesting case of a different kind of symbiosis called by the special name of **commensalism** (L. *com*, together + *mensa*, table), literally, eating at the same table, is that of a sea anemone which makes its home on the shell of a hermit crab enjoying the titbits which escape from its claws and at the same time camouflaging the crab's shell.

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   A. *Obelia* — A colonial hydroid 392
   B. *Gonionemus* — A hydroid medusa 394
   C. *Physalia* — A polymorphic hydrozoan 395
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3. A sea anemone, a type of the Anthozoa 397

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   A. The saclike type of structure 399
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   D. Colony formation 401
   E. Symbiosis 401

Questions

1. Compare the ectoderm and endoderm as regards their role in the animal's economy and cellular elements.
2. Describe the mechanism of the discharge of a nematocyst.
3. How does the coenosarc of *Obelia* receive its nourishment?
4. Briefly outline the life cycle of *Obelia.*
5. Compare a polyp of *Hydra* or of *Obelia* with the medusa of *Gonionemus.*
6. Discuss polymorphism in *Physalia.*
7. Compare the medusae of *Aurelia* and *Gonionemus.*
8. Briefly outline the life cycle of *Aurelia.*
9. Compare a sea anemone with a hydra.
10. Briefly outline the life cycle of sea anemone.
11. Discuss the classification of the Coelenterata.
12. Explain clearly what is meant by saying that the coelenterates have a saclike structure. Define diploblastic.
13. Compare the alternation of generations as found in the fern and in *Obelia.*
14. Compare budding and fission.
15. To what do coral islands owe their existence?

Suggestions for Further Reading

Hegner, Robert W., *Invertebrate Zoology*, The Macmillan Company, New York, 1933, Chap. III.

Buchsbaum, Ralph, *Animals without Backbones, An Introduction to the Invertebrates*, The University of Chicago Press, Chicago, 1938, Chaps. 7 and 8.

CHAPTER 20

Flatworms — Ectoderm, Endoderm, and Mesoderm, Bilateral Symmetry (Phylum Platyhelminthes)

In this chapter we will consider a phylum of animals which have evolved a plan of body structure more complex than the simple plan of the coelenterates and which show certain steps in the evolution of the higher animals. These steps consist of the development of (1) a cellular tissue between the ectoderm and endoderm so that the body of the animal consists of three layers, and (2) bilateral symmetry. To the three-layered condition the term **triploblastic** (Gr. *triploos*, triple + *blastos*, a sprout, here an embryonic layer) is applied. In this chapter types illustrating each of the three classes, Turbullaria, Trematoda, and Cestoda, will be described. The fourth class of the phylum, Nematoda, will not be discussed in this text.

1. A PLANARIAN

Planarians are small, elongated, flat, leaflike creatures which are found in fresh-water ponds clinging to or gliding over the underside of leaves (Fig. 20:1). *Euplanaria maculata*, the commonest fresh-water planarian, reaches a length of 15 millimeters. One end, the broader, is kept in advance as the animal moves through the water and is called the **anterior** end. The opposite end, called the **posterior**, is pointed. The upper, or **dorsal surface**, is spotted with black; the lower, or **ventral**

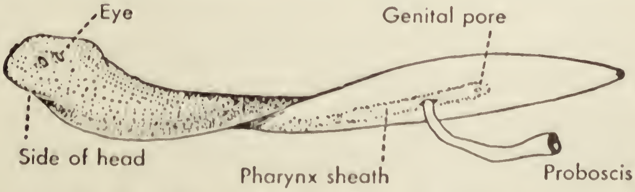

Fig. 20:1 *Planaria*, a fresh-water flatworm, with its probosis protruded. From Storer, *College Zoology*, McGraw-Hill Book Company, Inc.

surface, is white. A planarian is bilaterally symmetrical, that is, its organs and parts are arranged symmetrically on either side of the median plane which in this case extends from anterior to posterior and from dorsal to ventral along the median line. Most animals capable of active progressive movement are bilaterally symmetrical. Two **eyespots** appear on the dorsal surface of the head. The **mouth** opening is on the ventral side posterior to the middle of the animal. Posterior to the mouth is the small **genital opening.** The surface of the body is covered with cilia. The animal moves through the water by the coordinated beating of these cilia aided by an undulatory movement of the body

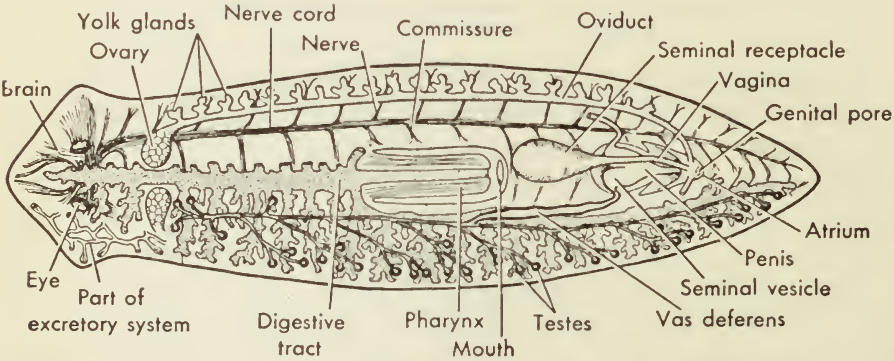

Fig. 20:2 *Planaria.* A general diagram to show the internal structure. Organs shown on the left are omitted on the right and vice versa. The gastrovascular cavity is here labeled digestive tract. From Storer, *General Zoology*, McGraw-Hill Book Company, Inc.

The mouth opens into a muscular **pharynx** which lies in a sheath extending anteriorly from the mouth. When irritated or in search of food, the planarian is able to protrude its pharynx from the ventral side of its body. The pharynx leads into the **gastrovascular cavity.** Immediately beyond its beginning, at the pharynx, this cavity divides into three main branches, one which extends anteriorly into the head giving off many branches, and two which extend posteriorly on either side of the pharynx to the extreme posterior end and which also on their way give off numerous branches (Fig. 20:2). Branches of this cavity thus extend to all parts of the body and distribute food material throughout their extent. These branches end blindly. There is no anus. The feces are passed out through the mouth. **Digestive juices** are poured into the gastrovascular cavity from cells in its walls. The digested food is absorbed by cells lining the gastrovascular cavity. Certain of these cells are also able, by means of pseudopodia, to **ingest solid food.**

The **excretory system,** like the digestive system, consists of a number of branching tubes extending to all parts of the body. From two small pores opening anteriorly on the dorsal surface, two **longitudinal tubes** extend down each side of the body. These give off numerous fine ramifying branches, each ending in the interior of a large **flame cell** (Fig. 20:3). The cavity of each flame cell contains a bunch of flagella which in life are in active movement. The actual excretion seems to take the form of secretion of waste products through the wall of the tube. The function of the flame cells appears to be to stir the liquid in the tube and prevent it from becoming too concentrated at the inner ends.

Respiration is carried on through the surface of the body.

The **nervous system** consists of two masses of nerve cells at the anterior end of the body from which two nerve cords extend posteriorly, one on either side, and give off branches to various parts of the body. A group of nerve cell bodies is called a **ganglion.** In the planarian the two groups of nerve cell bodies or ganglia are so closely associated that they are said to form a double ganglion which is called a **cerebral ganglion** or brain.

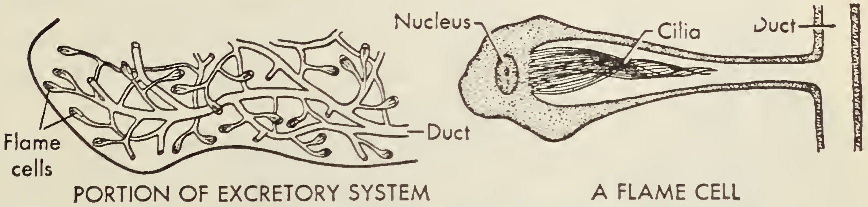

Fig. 20:3 *Planaria.* Part of the excretory system and one flame cell, both enlarged. After Lankester from Storer, *General Zoology*, McGraw-Hill Book Company, Inc.

The reproductive organs and the process of **sexual reproduction** of planarians, and of the flatworms in general, are complicated and will not be described in this text.

Asexual reproduction by **transverse fission** is common among planarians, the division to form the new individual usually occurring posterior to the pharynx. Planarians can be made to show in a very remarkable way the phenomenon of **regeneration** which, in various degrees, is rather widespread among organisms. If an individual is cut in two transversely, both the anterior and the posterior portions will grow into a complete animal. Even small pieces of a planarian may regenerate to form complete individuals.

Certain cells in the interior of the body of the planarian are developed into **muscle fibers.** Some of these run in a circular layer just beneath the surface of the body. Others run longitudinally. There is no skeleton.

As already noted, the finer branches of the digestive tract carry food to all parts of the body and the excretory system is also distributed throughout the organism. The need for a circulatory system, therefore, does not seem to exist. None is present, nor is there a body cavity. The spaces between the various organs are occupied by irregular cells to which the term **parenchyma** is applied.

2. LIVER FLUKES

A. THE LIVER FLUKE OF SHEEP, FASCIOLA HEPATICA

In general shape and in many details of structure, the liver fluke closely resembles the planarian (Fig. 20:4). Its mode of life is, however, very different. *Fasciola hepatica* in its adult stage lives as a parasite in the bile ducts of the liver of sheep, cows, pigs, and very rarely in man.

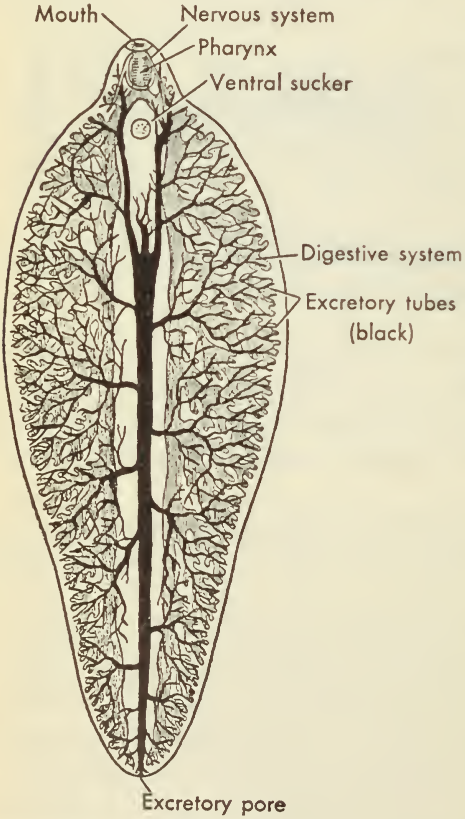

Fig. 20:4 Diagram of the digestive and excretory systems of the liver fluke, *Fasciola hepatica*. After Shipley and MacBride, *Zoology*, Cambridge University Press.

The **mouth** is at the extreme anterior end and is surrounded by a muscular disc forming the **anterior sucker.** A **ventral sucker,** not communicating with the digestive system, is situated a short distance posterior to the anterior sucker. The **genital opening** lies midway between the anterior and ventral suckers. The **excretory pore** is at the extreme posterior end of the body.

The digestive system, like that of the planarian, consists of branches ramifying to all parts of the body. The excretory and the nervous systems are also very similar to those of *Euplanaria.*

The liver fluke is hermaphroditic. The reproductive organs are very complicated and, in a sexually mature animal, occupy a considerable portion of its total volume (Fig 20:5). Fertilization is internal and usually the eggs and sperm come from different individuals. As many as five hundred thousand eggs may be produced by a single liver fluke.

Considerable interest attaches to the very complicated life history of the liver fluke. The **eggs** which have already started on a series of cell divisions before leaving the body of the parent pass out into the bile duct of the sheep and through its intestine to the outside world (Fig. 20:6 B). Only those eggs which reach fairly warm water continue to develop and become **ciliated larvae** (Fig. 20:6 D). These ciliated larvae which possess among other organs, a double eyespot, swim about in the water in search of a particular species of fresh-water snail. If they do not find it within 8 hours they die. If the ciliated larva reaches a snail it burrows into its body and there changes into a saclike **sporocyst** (Fig. 20:6 F) in which larvae of a second kind called **rediae** (Fig. 20:6 G, H) are produced. The rediae break through the wall of the sporocyst and bore into the tissues of the snail where they then, in turn, give rise to further generations of rediae. These rediae eventually in turn produce a third kind of larvae called **cercariae** (Fig. 20:6 I). The cercariae leave the

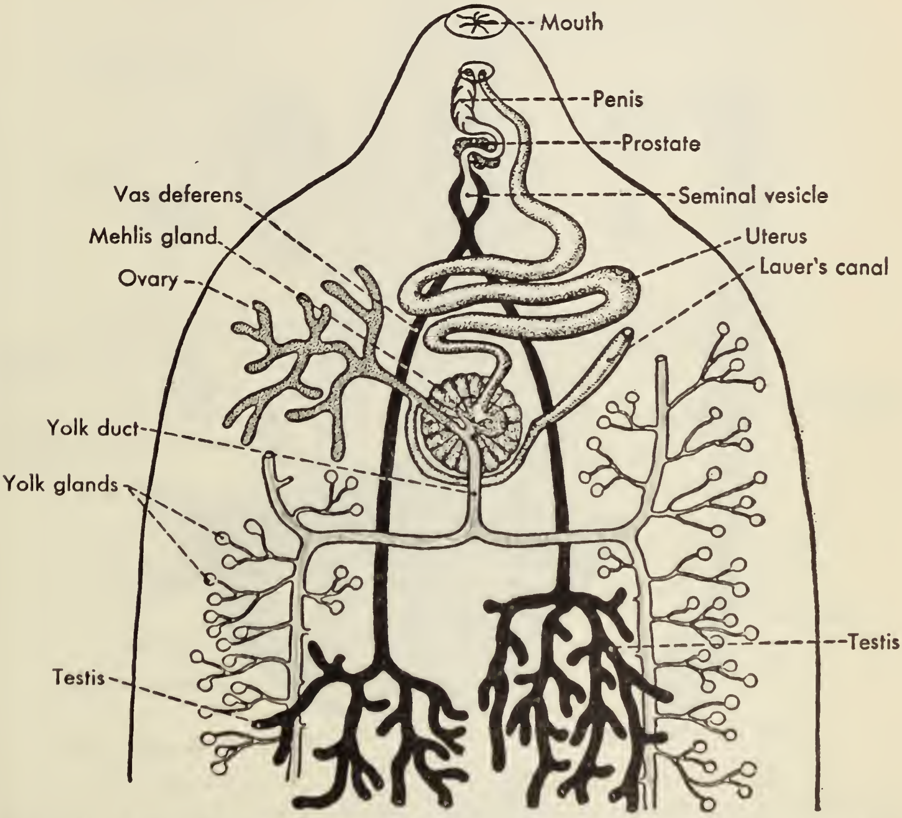

Fig. 20:5 *Fasciola hepatica.* Diagram of the anterior part of the body showing the reproductive organs. From Hegner, *College Zoology*, The Macmillan Company.

snail and after swimming about in the water **encyst** on leaves or on blades of grass (Fig. 20:6 K). If one of these leaves or blades of grass is eaten by a sheep and the cyst taken into its intestine, the cercariae emerge and find their way up the bile duct to the gall bladder where they develop directly into liver flukes. The method by which the various generations of rediae and cercariae are produced is called **parthenogenesis** (Gr. *parthenos*, a virgin + *genesis*, generation). The new individuals arise from special cells resembling ova but there is no union with a sperm cell to produce a zygote.

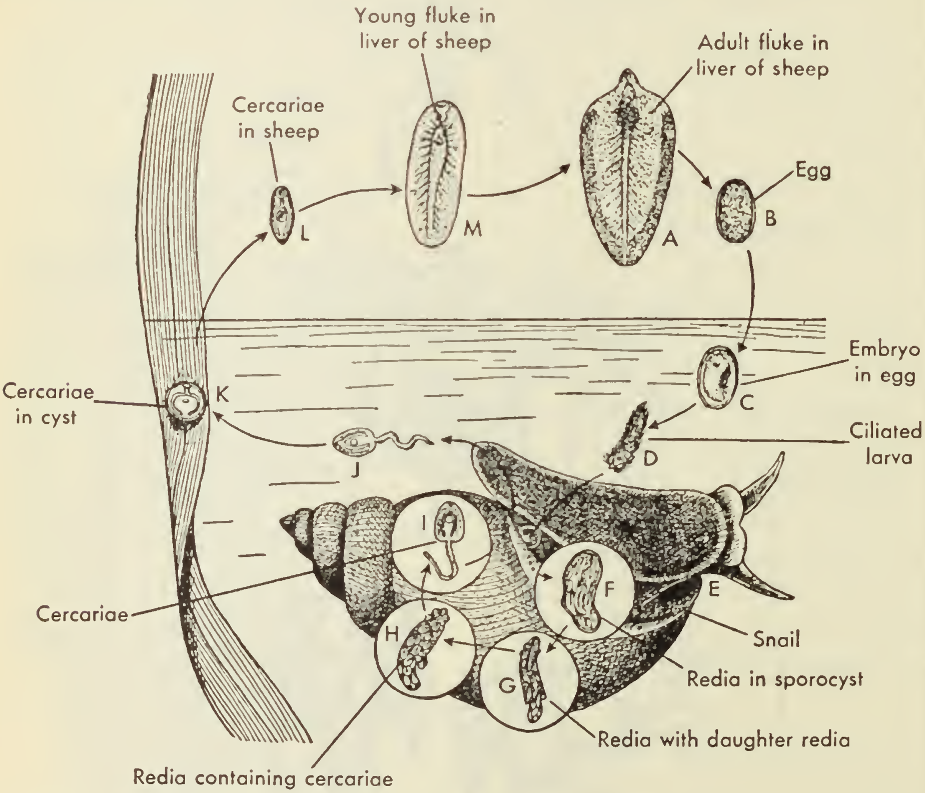

Fig. 20:6 The life history of the liver fluke, *Fasciola hepatica*. After A. C. Chandler, *Introduction to Human Parasitology*, by permission of John Wiley & Sons, Inc.

B. THE ORIENTAL LIVER FLUKE, CLONORCHIS SINENSIS

The most important liver fluke from the standpoint of human disease is the oriental liver fluke, *Clonorchis sinensis*. This fluke is widely distributed in the Far East where it is a common parasite of dogs, cats, pigs, as well as man. Man becomes infected from eating uncooked fish. The adult fluke which occurs in the hepatic ducts reaches a length of 25 millimeters or 1 inch. The arrangement of the internal organs is somewhat similar to that of *Fasciola hepatica.* However, the gastrovascular cavity is not divided up into small branches as in *Fasciola*, and there is a single median excretory canal (Fig. 20:7).

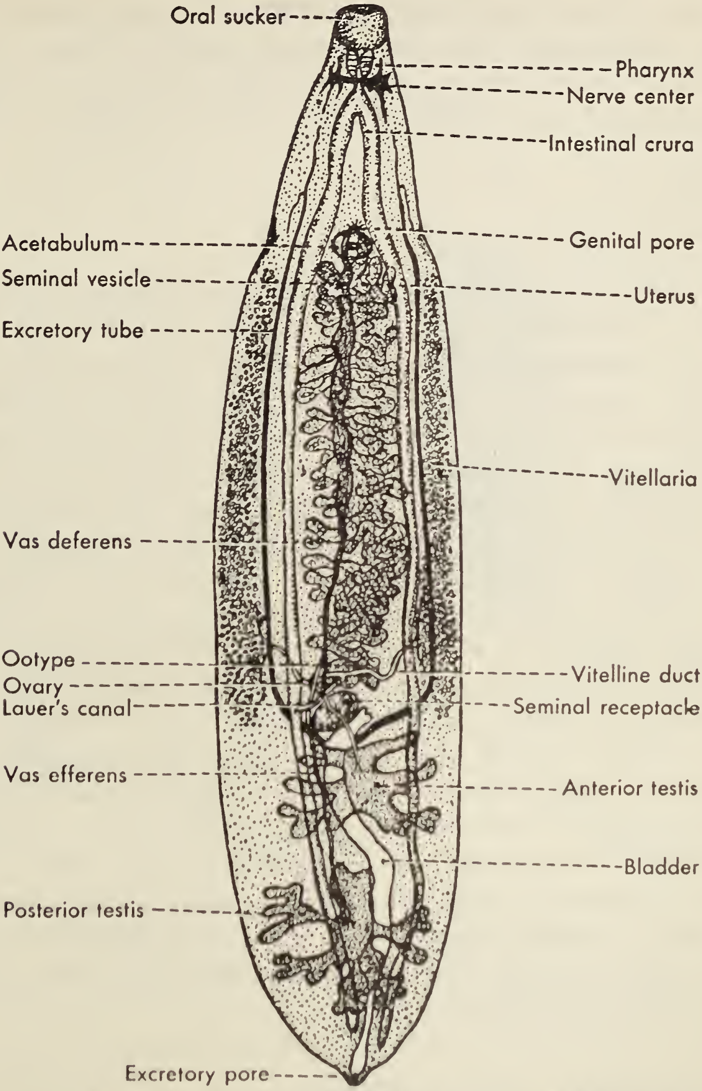

Fig. 20:7 *Clonorchis sinensis*, the oriental liver fluke of man. The branches of the gastrovascular cavity are here labeled intestinal crura. From Hegner, *College Zoology*, The Macmillan Company.

The **life cycle** involves two intermediate hosts. The minute eggs which pass out of the intestine of the host do not hatch unless they are eaten by a small pond snail. In the snail, the larvae, which hatch from the eggs, develop into sporocysts, which produce rediae, which, in turn, produce cercariae. These cercariae attack fresh-water fishes of the carp family, penetrating through the skin between the scales and entering the soft parts of the body. There they become encysted. When the fish is eaten by the mammalian host the young flukes are liberated in the intestine and find their way through the bile duct into the liver where they grow to maturity.

3. OTHER FLUKES

The blood fluke, *Schistosoma haematobium*, is an important human parasite living in the blood. It is common in Africa and Madagascar, and occurs in southwestern Asia, southern Europe, and Australia. Egypt seems to be especially concerned, 70 to 80 per cent of the population being infected. According to one authority it "is accountable more than anything else for the indolence of spirit, want of character, and backward condition of the Egyptian peasant."[1] The intermediate hosts are snails which inhabit rivers and ponds. Infection is through drinking water. A specific treatment has been discovered in the drug, tartar emetic, which when injected into the blood stream kills the parasite.

In many parts of the Far East, including Korea, Japan, Formosa (where 40 to 50 per cent of the population are infected), Indo-China, Siam, Philippines, Malaya and parts of India, and also in New Guinea, Peru, Venezuela, Yucatan, and in parts of the United States a serious disease of man and animals is caused by **lung flukes** of the genus *Paragonimus*. The life cycle of these parasites includes two intermediate hosts, occupied in succession; the ciliated larvae infect snails where the development proceeds to the cercaria stage. The cercariae attack fresh-water crabs, or in the United States, where no fresh-water crabs are known to occur, crayfish. Infection usually comes from eating uncooked, infected crabs or crayfish.

4. A TAPEWORM, *TAENIA SOLIUM*

Taenia solium is the pork tapeworm. Its immature stages occur in the pig, especially in the muscles of the tongue, neck, heart, shoulder, and hams. The sexually mature stage occurs in the intestine of man. Infection is caused by the eating of insufficiently cooked pork. Man is the only animal known to serve as the final host. It is fairly common in cer-

[1] Christopherson, quoted by Chandler in *Introduction to Human Parasitology.*

tain localities in Europe but is rare in most parts of the United States and in countries where there is a religious ban on eating pork.

A tapeworm (Fig. 20:8) consists of a "head" or **scolex,** scarcely as large as the head of a pin (about 1 millimeter in diameter), a short, thin **neck,** and a number of flattened segments called **proglottids.** The head is armed with a ring of from twenty-two to thirty-two small hooks and four sucking discs by means of which it attaches itself to the wall of the intestine of its host, in this case man. A specimen of *Taenia solium* from the human intestine may reach a length of from 6 to 10 feet.

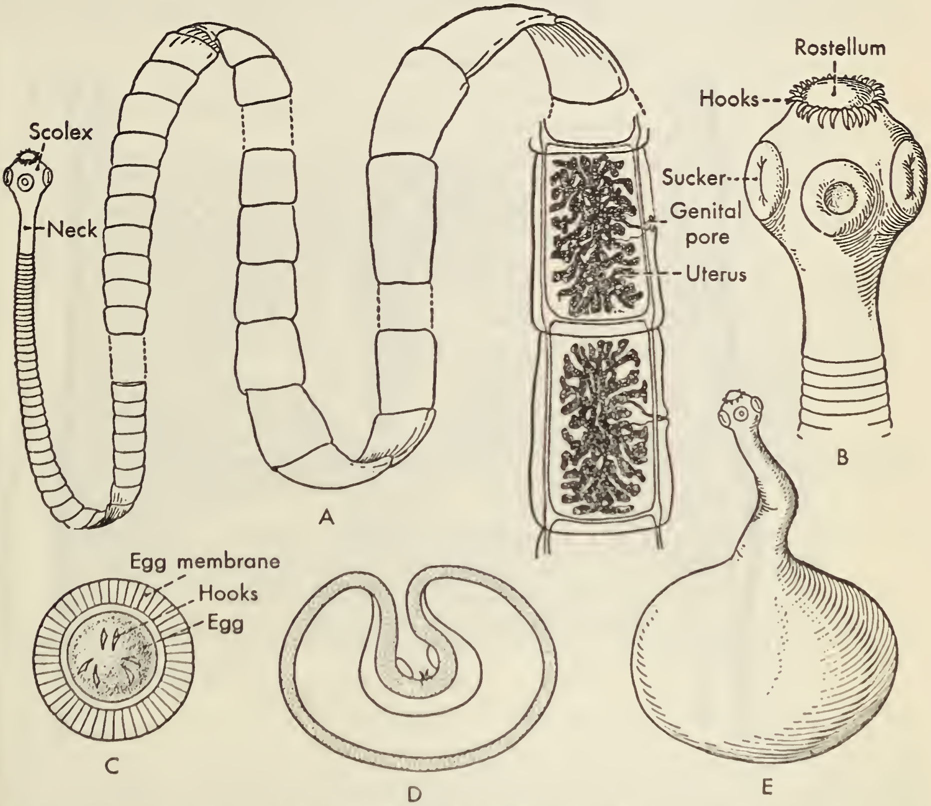

Fig. 20:8 *Taenia solium,* a tapeworm of the pig. A, specimen about 8 feet long consisting of about 900 proglottids, with four sections omitted; the uterus filled with eggs is shown in the last two proglottids; about four times natural size. B, scolex, magnified about thirty-five times. C, egg surrounded by a membrane and bearing six hooks. D, bladderworm or cysticercus with scolex at bottom of invagination. E, cysticercus with head evaginated and ready to become attached to the intestinal wall. From Hegner, *College Zoology,* The Macmillan Company.

The proglottids are produced in the region just behind the neck by a process analogous to budding, resembling the way in which medusae are formed by the strobila of the Scyphozoa. The youngest proglottids are those nearest the neck and the oldest those furthest away. Each proglottid contains all the organs necessary to carry on its existence and reproduce the species. Nevertheless, the nervous and excretory systems extend throughout the length of the tapeworm.

The food of the tapeworm is already digested for it by the digestive juices of its host. This digested food it absorbs through the entire outer surface of its body. There is no internal digestive system in the scolex or in the proglottids, either in the form of a digestive cavity or digestive glands.

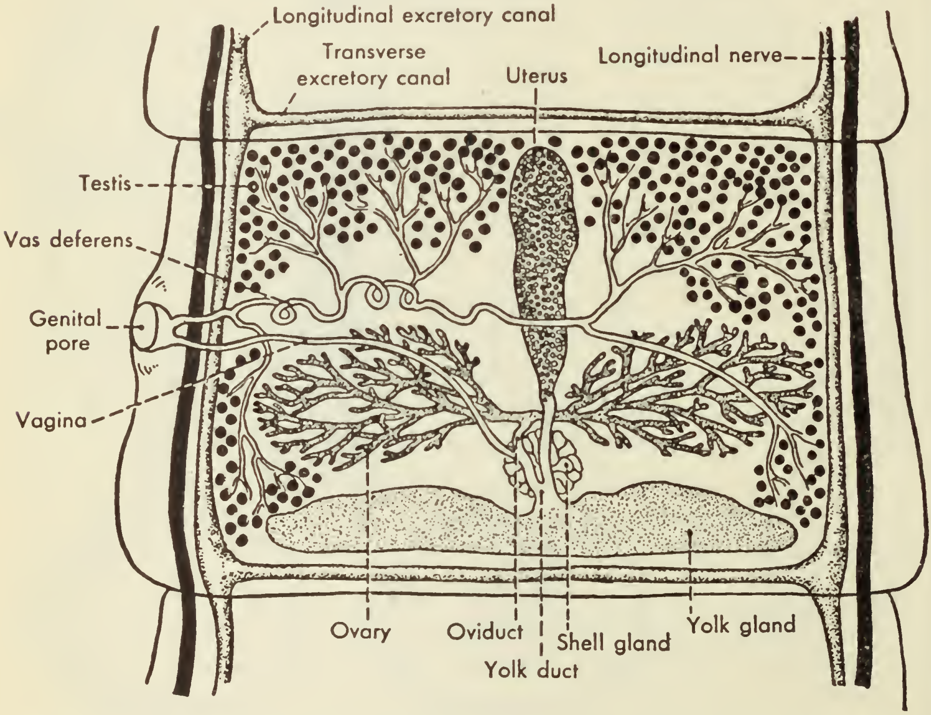

Fig. 20:9 *Taenia solium.* A ripe proglottid showing the reproductive organs, nerves, and excretory canals. From Hegner, *College Zoology*, The Macmillan Company.

The **excretory system** is like that of the liver fluke and planarian. It consists of a branching system of tubes ending in flame cells. The **nervous system** is essentially similar to that of the planarian and liver fluke and consists of a pair of ganglia in the scolex from which arise nerve cords which run the entire length of the worm. There are no sense organs. Each proglottid has a complete set of **reproductive organs** and is, therefore, termed **hermaphroditic.** Like the reproductive organs of the planarian and fluke, they are quite complicated. The reproductive organs occupy most of the proglottid, which when mature is little more than a sac of eggs (Fig. 20:9). As the proglottids become mature and filled with ripe eggs, they become separated from the rest of the worm and pass out of the intestine on to the ground.

An interesting question arises regarding the tapeworm: Is the entire tapeworm one individual or are the separate proglottids individuals which are associated to form a colony? Probably the latter interpretation is the more correct since each proglottid would undoubtedly be capable of an independent existence had it some separate means of attachment or other means of staying in the intestine.

A man infected with a single tapeworm may expel several ripe proglottids per day, each containing thousands of eggs. Each of these eggs contains a small embryo armed with three pairs of hooks. The further development of these embryos depends on their being ingested by another host, usually the pig, although it may be a man if his food becomes contaminated with the eggs. The embryos then bore through the wall of the intestine and make their way or are carried in the blood to the muscles. After arriving in the muscles they grow into "bladder worms" or **cysticerci** (Fig. 20:10). As the name "bladder worm" implies, this stage is bladderlike. The head of the tapeworm is developed inside the bladder. When uncooked pork or other meat containing bladder worms is eaten, the young scolex, liberated in the intestine of a man or a pig, attaches itself and forms proglottids.

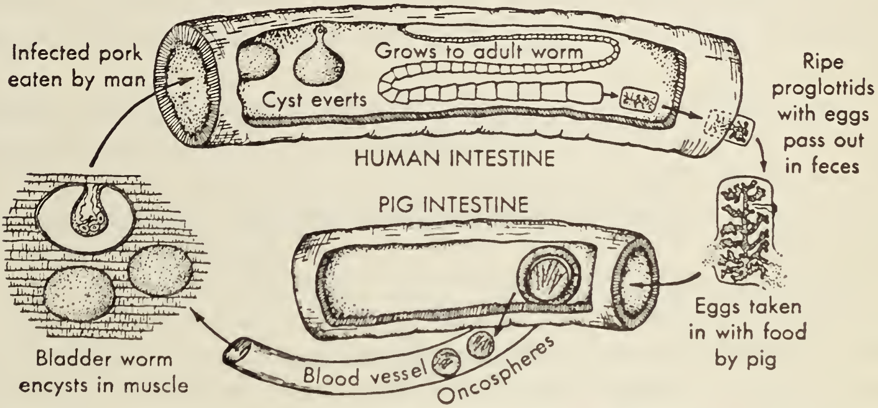
Infected pork eaten by man
Cyst everts
Grows to adult worm
Ripe proglottids with eggs pass out in feces
HUMAN INTESTINE
PIG INTESTINE
Eggs taken in with food by pig
Bladder worm encysts in muscle
Blood vessel
Oncospheres

Fig. 20:10 *Taenia solium.* Diagram of life cycle. From Storer, *General Zoology*, McGraw-Hill Book Company, Inc.

5. OTHER TAPEWORMS

Four species of tapeworm occur fairly frequently in the adult stage (proglottids) in man. They are the fish tapeworm, *Diphyllobothrium* *latum;* the pork tapeworm, *Taenia solium;* the beef tapeworm, *Taenia saginata;* and the dwarf tapeworm, *Hymenolepis nana.*

The fish tapeworm, ***Diphyllobothrium latum***, occurs in central Europe, the Baltic countries, central Asia, Manchuria, Japan, Madagascar, and in a few places in Africa and North America. It is the largest of the human tapeworms, reaching a length of over 30 feet. There are two intermediate hosts. The ciliated larvae are eaten by small crustaceans of the genus *Cyclops* in the body cavities of which they undergo a part of their development. When the cyclops is eaten by a fish the larvae burrow through the intestine and reach the muscles. There they develop into elongated wormlike animals with an inverted scolex. When uncooked infected fish is eaten by man the scolex is everted, the tapeworm becomes attached to the intestinal wall, and proglottids begin to be formed.

The life history of the beef tapeworm, ***Taenia saginata***, closely parallels that described for *Taenia solium* with cattle as the intermediate hosts in place of pigs. The muscles of the jaws and heart are the parts of the beef most commonly infected and it is these parts which are usually examined in meat inspection. Cattle become infected by the ingestion of the eggs of the parasite. In Europe and America where cattle are kept under fairly hygienic conditions, infection is rare, but in the tropics where cattle often eat human fecal matter, the bladder worms may be very numerous. *Taenia saginata* is widely distributed but is especially common in parts of Africa, Syria, and Tibet where raw or partially cooked beef is eaten. It is exceedingly rare among Hindus since their religion prohibits beef eating.

The dwarf tapeworm, ***Hymenolepis nana***, is a small, short worm. It is peculiar in that its entire life cycle takes place in a single host, the embryos boring their way into the wall of the intestine and developing there into a bladder-wormlike stage from which they emerge into the intestine again as adults. The distribution of the dwarf tapeworm is world wide. "It is the commonest tapeworm in the southern United States, where about 1 to 2 per cent of the population, especially children, are infected. In Europe it is especially common in Italy. In India as high as 18 to 28 per cent of the population was found by the writer to be infected."[1]

Two species of tapeworm occur fairly commonly in man in the larval stage. They are *Taenia solium*, already referred to, and *Echinococcus granulosus*, the enormous bladder worms of which are known as hydatid cysts. The adult, ***Echinococcus granulosus***, is a minute worm, resembling

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[1] Chandler, *Introduction to Human Parasitology.*

Taenia solium in structure, which is very common in the intestines of dogs. The eggs or ripe proglottids are expelled in the feces of infected dogs. Other mammals besides man may act as the host of the larva. Human beings become infected through the drinking water or handling infected dogs. Children are more commonly infected than adults from kissing dogs or allowing them to lick the face. The eggs hatch in the intestine. The larvae bore through the intestinal wall and enter the blood stream in which they are carried about. They usually become caught in the capillaries of the liver or lungs and there begin to form bladder worms or cysts. The cysts grow very slowly but may continue for years, reaching an enormous size. *Echinococcus granulosus* is most frequent in sheep and cattle countries since these animals may serve as hosts for the larvae, and dogs are used for herding. Human infection is common in Iceland, Africa, Australia, and South America south of Brazil. The only treatment for the disease is the surgical removal of the hydatid cysts when this is possible.

6. BIOLOGICAL PROBLEMS ILLUSTRATED IN THE PLATYHELMINTHES

A. THE PLAN OF STRUCTURE OF THE PLATYHELMINTHES

The plan of structure of the Coelenterata, as we saw in the previous chapter, is that of a sac enclosed by two layers of cells, the gastrodermis and the epidermis, separated by the noncellular mesoglea. In the Platyhelminthes, with the exception of the tapeworms where a digestive tract is lacking, this saclike structure of the digestive tract is also evident. However, in place of mesoglea there is a thick mass of cellular tissue in which numerous organs such as the excretory and reproductive organs are developed. This middle layer of tissue which develops between the ectoderm and endoderm is called the **mesoderm** and the three-layered condition which results is termed **triploblastic.**

Food materials are transported to the cells of the different organs in the many branches of the digestive tract. The waste products of the metabolism of the cells are excreted by the flame cells and carried to the exterior in the tubules of the excretory system. The reproductive organs are internal and in consequence have developed a series of ducts.

B. BILATERAL SYMMETRY

The members of this group possess bilateral symmetry. This is an important step in evolution since it involves the differentiation of anterior and posterior ends and coordinated movements in locomotion.

C. PARASITISM

Although parasitic species occur in practically all the different phyla of animals and in many plants, it is convenient to discuss the general subject of parasitism at this point, since so many of the striking features of parasitism are especially well illustrated in the Platyhelminthes.

(1) THE ORIGIN OF PARASITISM

It is not possible to be certain in any particular case exactly how a parasitic species arose. However, it is generally believed, and there is much evidence for the thesis, that parasites evolved **from related free-living species.** One kind of evidence is that all stages between a free and independent existence and complete parasitism are frequently found in different species of the same group or related groups. Thus the structure of the Turbellaria and Trematoda clearly shows that they are closely related groups, the one free-living, the other parasitic. Add to this the fact that some species of turbellarians are semiparasitic. One such lives attached to the gills of the king crab, *Limulus*, while another lives in the mouth cavity of a gastropod mollusk.

(2) TYPES OF PARASITISM

Some parasites are found attached to the external surface of the bodies of their hosts and are therefore called **ectoparasites;** while others, called **endoparasites,** occur inside the body in cavities such as those of the digestive, respiratory, and vascular systems, or in tissues such as those of the muscles and brain. Thus the turbellarian referred to above as living on the gills of the kingcrab is an ectoparasite; the liver fluke is an endoparasite living in a cavity, while the cysticercus-stage of the beef tapeworm is a **tissue parasite**.

(3) ADAPTATIONS TO PARASITISM

The body of the host forms the environment for the parasite and the latter must be adapted to this environment. There is thus a **host-parasite relationship** with the result that most parasites are restricted to a few host species. In general it is to the advantage of the parasite to cause as little disturbance as possible in the body of its host. When a parasite kills its host this is usually due to imperfect adaptation, for in doing so it is indeed killing the goose which lays the golden egg. **Adaptation** is also important in the transfer of the parasite from host to host. This will be referred to later under reproduction and life cycles.

(4) "DEGENERACY" IN PARASITES

From our point of view parasites are degenerate creatures. From the parasite's point of view, if it had one, which it does not, the host is merely a source of livelihood. However, the dependent existence of the parasite on or in the body of another organism is accompanied in a greater or less degree by the **loss of organs** or other structures no longer useful. This is particularly true of sense organs. Thus, although the ciliated larva of the liver fluke possesses an eyespot, which presumably helps it to find its host snail, the adult fluke lacks any such organ. In the adult tapeworm the digestive tract is entirely lacking.

(5) REPRODUCTION AND LIFE CYCLES

Parasitic worms lay **incredible numbers of eggs** which are usually contained in protective coatings. With this is correlated a rather **complicated reproductive system** which occupies a large place in the body. This is well illustrated in the liver fluke and the proglottid of the tapeworm. Also, frequently, the immature stages multiply by asexual reproduction. This is seen in the formation of rediae and cercariae in the life cycle of the liver fluke and in the cysticerci of many tapeworms in which numerous heads are formed.

Some parasites are able to complete their life cycle in a single host. Examples of this are frequent among the roundworms and will be described in the next chapter. Many parasites require two entirely different hosts and a few require or usually have three different hosts. It is usual to call the host of the adult stage of the parasite in which sexual reproduction occurs the **final host** and the host of the immature stages the **intermediate host**. The presence of an intermediate host ensures, at least in certain cases, a wider dispersal of the parasite.

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Questions

1. Compare the digestive system of *Planaria* with that of *Hydra.*
2. Why is an excretory system necessary in *Planaria?*
3. Describe a flame cell. Why does it contain cilia?
4. Compare the nervous system of *Planaria* with that of *Hydra.*
5. Describe the life history of the liver fluke.
6. What advantages and disadvantages are there for the liver fluke in having a number of different stages in its life history?
7. Define parthenogenesis. Can you give any reason for its occurrence in the liver fluke?
8. Why is a digestive system absent in the tapeworm?
9. Discuss the question whether the tapeworm is a colony or an individual.
10. How may infection with the tapeworms be avoided?

Suggestions for Further Reading

Hegner, Robert W., *College Zoology*, The Macmillan Company, New York, 1942, Chap. XII.

Buchsbaum, Ralph, *Animals without Backbones, An Introduction to the Invertebrates*, The University of Chicago Press, 1938, Chaps. 12 and 13.

Chandler, Asa C., *Introduction to Human Parasitology*, John Wiley & Sons, Inc., New York, 1930, Chaps. XII and XIII.

Ward, H. B., and G. C. Whipple, *Fresh-Water Biology*, John Wiley & Sons, Inc., New York, 1918, Chap. XII, "The Free-Living Flatworms" by C. E. Stringer; Chap. XVI, "The Parasitic Flatworms" by H. B. Ward.

CHAPTER 21

The Roundworms — Tube-within-a-tube Type of Body (Phylum Nemathelminthes)

The step in the evolution of the higher animals which this phylum illustrates may be designated the "tube-within-a-tube" type of body structure. In this type of structure the body of the animal consists of an outer tube, called the **body wall,** which surrounds a cavity within which is another tube called the **digestive tube,** alimentary canal, or digestive tract, opening at one end of the animal by a mouth and at the other end by an anus. The material to be digested is taken in at the mouth and the unabsorbed residue is passed out at the anus as the **feces,** the process of evacuation of this material being called **defecation.**

1. ASCARIS

As an example of this phylum, we take a parasitic roundworm, *Ascaris lumbricoides*, found in the intestines of horses, pigs, and man. It should be noted in passing that many, perhaps most of the Nemathelminthes, are free living. *Ascaris* is chosen on account of its large size (it reaches a length of 25 centimeters, 10 inches) and the ease with which it may be dissected. The species name *lumbricoides* refers to the resemblance to the earthworm Lumbricus. *Ascaris*, however, is not divided into ringlike segments like the earthworm and, like most internal parasites, it is white in color. The elongated body is pointed at both ends. At the extreme tip of one end, which, on this account, is distinguished as the anterior, is the **mouth,** a triangular opening surrounded by **three lips.** A short distance from the other end is the **anus.**

If the body wall of *Ascaris* be cut open, it will immediately be discovered that it contains a relatively large fluid-filled cavity extending the entire length of the body and containing various organs (Fig. 21:1). This cavity is referred to as a **pseudocoel,** because the body cavity of *Ascaris* and of the Nemathelminthes in general differs in certain respects from a true body cavity as seen in the higher animals. Typically a coelom is lined with an epithelium developed in the embryo from the middle layer or mesoderm, the germ cells arise from its wall, and the excretory organs, at least in their embryonic stages, open into it. In *Ascaris* the cavity is lined by mesoderm only on the surface toward the body wall; there being no mesoderm covering the digestive tract, the germ cells are not developed from its lining, and the excretory organs do not open into it.

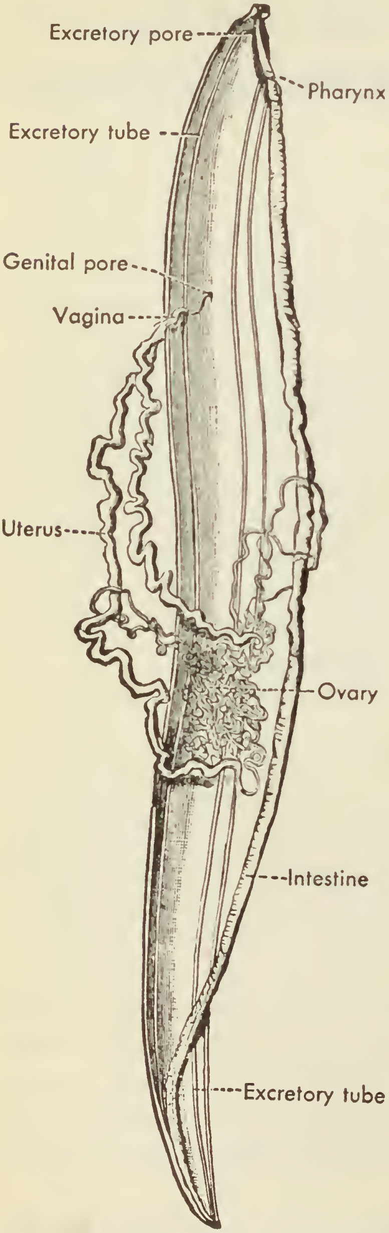

Fig. 21:1 *Ascaris lumbricoides.* A female cut open to show internal organs. After Shipley and MacBride, from Hegner, *College Zoology*, The Macmillan Company.

Among the various organs in the body cavity is the **digestive tract** which consists of a straight tube running from the mouth to the anus. *Ascaris* illustrates especially clearly what has been called the **tube-within-a-tube** type of animal body. The body cavity between the two tubes is closed by the fusion of the wall of the outer tube, of ectodermal and mesodermal origin, with the wall of the inner tube, in *Ascaris*, of endodermal origin only, at the mouth and anus. The mouth is found to lead directly into a muscular **pharynx** with which the already digested materials from the intestine of the host are sucked in. This is followed by a long straight **intestine** consisting of a single layer of columnar epithelial cells by which the nutrient materials are absorbed and passed into the body fluid in which they are distributed to all parts of the body, there being no circulatory system such as occurs in the higher animals. Just before the anus the intestine narrows to form a short **rectum.** In the male a **cloaca,** which is continuous with the rectum and into which the genital duct opens, intervenes between the rectum and the anus.

The body wall is developed from ectoderm and mesoderm (Fig. 21:2). The outer surface is covered by a **chitinous cuticle** secreted by the epidermis. The epidermis of *Ascaris* takes the form of a **syncytium,** i.e., it consists of numerous nuclei scattered in a continuous layer of protoplasm not divided into separate cells. Within the epidermis and bounding the body cavity is a layer of large **muscle cells** which are developed from the mesoderm. These muscle cells are of considerable interest as they are believed to show how the more specialized muscle cells of higher animals may have been evolved (Fig. 21:3). The contractile portions of these cells lie immediately under the epidermis and extend longitudinally. The cell bodies appear in cross sections as rounded masses projecting into the body cavity (Fig. 21:2). Muscle cells are absent and the epidermis is thickened along four longitudinal lines extending the

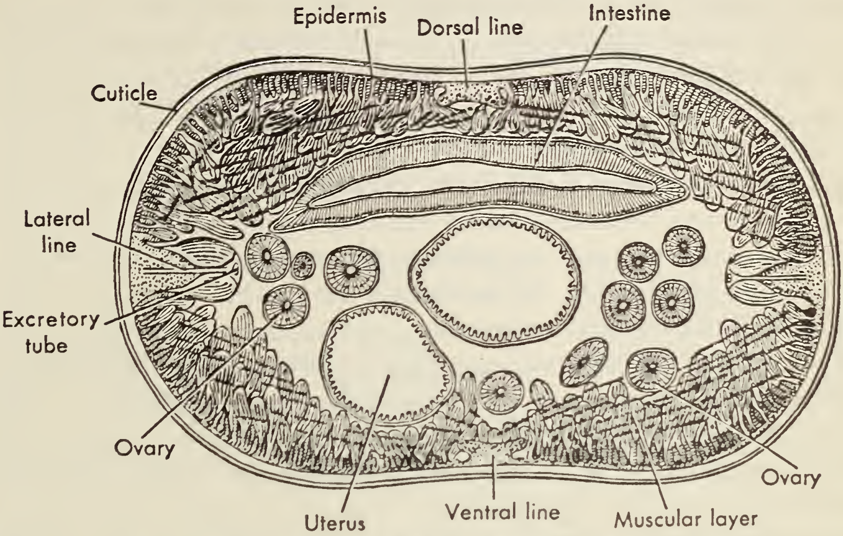

Fig. 21:2 *Ascaris lumbricoides,* transverse section. After Parker and Haswell, after Vogt and Yung. From Hegner, *College Zoology,* The Macmillan Company.

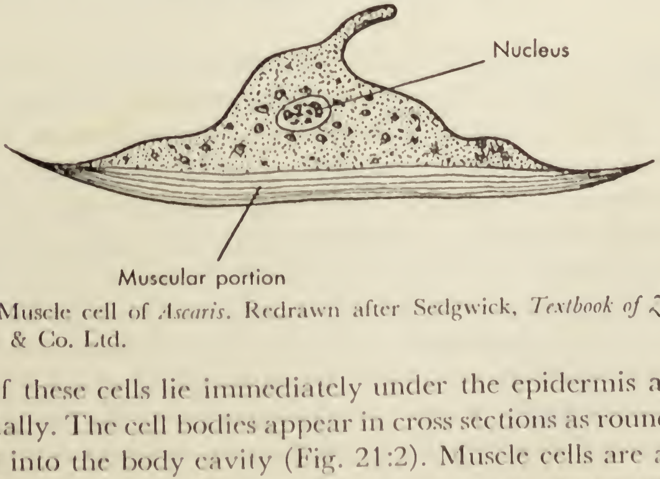

Fig. 21:3 Muscle cell of *Ascaris.* Redrawn after Sedgwick, *Textbook of Zoology,* Swan Sonnenshein & Co. Ltd.

length of the body. Two of these lines are lateral, one dorsal, and one ventral.

Two tubes which run in the lateral lines and open to the exterior by a single pore in the anterior region have been called **excretory tubes** and assigned an excretory function. Recent investigations have shown, however, that their having such a function is extremely doubtful, and that **excretion** is probably carried on by the body wall, the waste products being carried to the body wall from the other parts of the organism in the fluid of the body cavity.

The **nervous system** consists of a **ring of nervous tissue** surrounding the pharynx and two **nerve cords** running, one in the dorsal line of the thickened epidermis, and the other in the ventral line.

The sexes are separate. In the **female** the **genital opening** is a small transverse slit in the mid-ventral line at about one-third of the length of the worm from the anterior end. It leads into a short tube called the **vagina** which divides into two long convoluted tubes. Each of these tubes is differentiated into three portions, the portion nearest the vagina has the largest diameter and is called a **uterus,** the middle portion is an **oviduct,** and the thin upper portion is the **ovary.** Each ovary may contain as many as a million eggs, 200,000 of which may be laid in a single day. The eggs are fertilized in the lower ends of the oviducts. In the **male** the reproductive system consists of a single long tube differentiated along its length. The upper portion which is long, coiled, and threadlike forms the **testis** in which sperms are formed. Leading from the testis is the **vas deferens** which is continued by a somewhat wider tube, the **seminal vesicle,** in which the spermatozoa are stored. From the seminal vesicle a short muscular **ejaculatory duct** leads into the **cloaca.**

The **eggs** do not begin their development until they have left the female and the host. They are extremely resistant to many chemical substances and may retain their capacity to develop over a period of years. Infection of a new host usually occurs by the swallowing of eggs. When the eggs are swallowed by a horse, pig, or man, the embryos hatch in its small intestine. From the intestine the young worms go on a ten-day tour, a sort of "homeseeker's trip through the body." They penetrate the mucous membranes and are carried by the blood stream to the liver, then to the heart, and then to the lungs. From the blood vessels of the lungs they work their way out into the cavities of the lungs and eventually find their way through the throat and esophagus back to the intestine. During the trip they grow to about ten times their length at starting.

2. OTHER NEMATHELMINTHES

The Nemathelminthes are a very numerous and widely distributed phylum. The free-living species occur almost everywhere, on land, in the sea, and in fresh water. They occur as parasites in both plants and animals. In some cases they are relatively harmless, in other cases they cause serious and even fatal diseases. In the latter category are the trichina worm and the hookworms.

The trichina worm, *Trichinella spiralis*, is the cause of a muscular disease in man called **trichinosis.** This disease used to be much more frequent than at present. It is now rather rare in the United States, thanks to the wide publicity given to the evil effects of eating raw or insufficiently cooked pork. Serious epidemics have occurred in Germany, Austria, and Italy where sausages containing raw pork are popular. Man becomes infected by eating raw meat containing encysted larvae of the worm. The larvae come out of their cysts in the intestine. Here they mature and the adults (Fig. 21:4) mate. The females burrow into the intestinal wall and deposit their living young in a lymph or blood vessel. The minute larvae are carried all over the body in the blood stream. They soon leave the capillaries and enter the fibers of the striated or voluntary muscles, particularly those of the diaphragm, chest, and tongue. There they grow rapidly in size and become surrounded by a hard resistant cyst from which they become liberated only when eaten by another host. Besides man and hogs the trichina worm also infects rats and mice. There is no known cure for trichinosis, which frequently results in death. To destroy the parasites the pork must be thoroughly cooked; red or raw portions left in the center of either boiled or roasted pork may contain living larvae and cause infection.

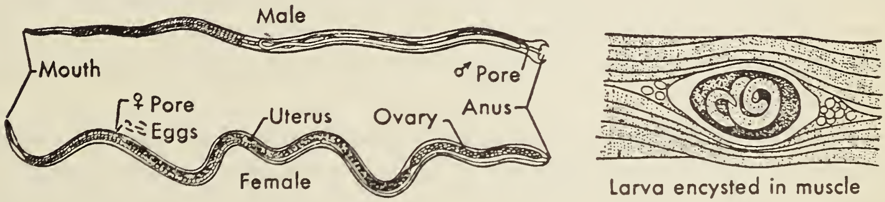

Fig. 21:4 *Trichinella spiralis*, the trichina worm, cause of trichinosis. From Storer, *General Zoology*, McGraw-Hill Book Company, Inc.

There are two species of **hookworm.** The New World species is *Necator americanus*. This is the well known hookworm which is widely distributed in the southern states. The Old World species is *Ancylostoma duodenale*. With the possible exception of the malaria parasite the different species of hookworm are probably responsible for more human misery and death than any other animal parasite. The adult hookworms of both *Necator* and *Ancylostoma* live in the small intestine from the wall of which they suck blood and lymph. A single worm may produce as many as ten thousand eggs per day, which are passed out of the host in the feces. Embryos hatch in about 24 hours, grow rapidly, and at the end of about 5 days have become small larvae 1/2 millimeter in length. The larvae live on the surface of the soil and infection takes place when they bore their way through the skin, usually that of the bare foot. From the skin the larvae enter blood vessels and are carried to the lungs where they bore their way out into the air spaces. From the lungs they reach the throat and if swallowed with the food arrive in the intestine where they acquire a mouth and start feeding. A single worm may live for five or more years in the intestine.

The hookworm disease is a tropical and semitropical disease, extending through central Africa, India, Siam, Malaysia, southern China, northern South America, Central America, and the southern United States. Its effect is "insidious; year after year, generation after generation, it saps the vitality and undermines the health and efficiency of whole races of people."[1] Carbon tetrachloride taken by mouth has proved an effective treatment for ridding the intestine of the worms. The use of privies, disinfecting the soil, and the wearing of shoes or boots to protect the feet are important preventive measures.

Another species of Nemathelminthes of considerable importance in tropical countries is the filaria, *Wuchereria bancrofti*. The adults which reach a length of 3 to 4 inches but are scarcely thicker than a piece of thread, live in the lymph glands of man where their presence causes a peculiar disease called **elephantiasis,** in which the lymph glands may be swollen to an enormous extent. Infection is by means of an intermediate host, a mosquito. The worms breed in the lymph glands and produce larvae called **microfilariae** which, to continue their development, must be transferred to a mosquito. In the course of from 10 days to several weeks in the mosquito the larvae develop into worms which are transferred to the human host when the mosquito bites.

Species of Nemathelminthes attack various food plants such as the beet, tomato, turnip, and potato and are the cause of some loss to the farmer.

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[1] Chandler, A. C., *Introduction to Human Parasitology.*

3. BIOLOGICAL PRINCIPLES ILLUSTRATED IN THE NEMATHELMINTHES

With the development of a body cavity in *Ascaris*, the tube-within-a-tube type of body came into existence. The outer tube or body wall, as already stated, is composed of ectoderm and mesoderm. The ectoderm maintains contact with the outside world. This is a comparatively simple matter in a parasite since its environment does not change except during its immigration; hence in parasitic animals sense organs are usually lacking or much reduced. The mesoderm of the body wall takes on, as one of its functions, the movement and locomotion of the animal. In *Ascaris*, as already stated, muscle cells are developed in it. The body cavity of *Ascaris*, while it does not correspond to the coelom of the higher animals, occupies the same general position in the tube-within-a-tube plan of body. The inner tube consists in *Ascaris* of endoderm only. Generally in animals, the endoderm is concerned with the functions associated with digestion and secretion.

The Nemathelminthes, like the Platyhelminthes, contain many parasitic species and illustrate well many of the features of parasitism, which are discussed in detail at the end of the chapter on the Platyhelminthes.

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3. Biological principles illustrated in the Nemathelminthes 425

Questions

1. Explain clearly what is meant by the "tube-within-a-tube" type of body structure and show how this applies to *Ascaris*.
2. How does the body cavity of *Ascaris* differ from the coelom of a higher animal?
3. Why would you not expect to find digestive glands in *Ascaris?*
4. How are the nutrient materials distributed throughout the body of *Ascaris?* Compare this method with that in *Fasciola* or *Planaria*.
5. Briefly outline the life history of *Ascaris*.
6. Name some of the more important Nemathelminthes parasitic in man.

Suggestion for Further Reading

Chandler, Asa C., *Introduction to Human Parasitology*, John Wiley & Sons, Inc., New York, 1930, Chaps. XIV–XVIII.

CHAPTER 22

The Segmented Worms — A True Coelom and Metamerism (Phylum Annelida)

The segmented worms, of which the common earthworm, *Lumbricus terrestris*, is an example, show two important steps in evolution — the development of a true coelom and metamerism. As already stated in Chap. 21, the body cavity which is found in the Nemathelminthes or roundworms is not regarded as a true coelom. A true coelom is a cavity which is lined by an epithelium developed from the mesoderm or middle germ layer in the embryo (see Chap. 36). The body cavity of annelids conforms to this definition. It lies between the digestive tract and the body wall. In many animals the excretory organs, known as nephridia, open internally into the coelom, and the reproductive cells can be shown to originate from a portion of the epithelium which lines its walls. This description applies to the body cavity of annelids. Another striking feature in the structure of annelids is the transverse division of the body into a series of disc-shaped segments. In general these segments or metameres are similar throughout the length of the body, so that each of the main organ systems, with the exception of the reproductive organs, consists of a repetition of similar parts arranged in a longitudinal series, one part in each segment. This repetition of similar parts of an organ system in successive segments of the body is called **metamerism.** It is especially well illustrated in the annelids and the next phylum, the arthropods. It occurs in the higher animals, even in ourselves, but is there restricted to certain organs and is less apparent. The metamerism of an animal like the earthworm differs from the condition found in the tapeworm. The metameres of the earthworm develop simultaneously in the embryo and are not budded off from a growing region as in the tapeworm. The earthworm is an individual divided into metameres; the tapeworm is properly regarded as a colony of individuals, each of which is represented by a proglottid.

1. THE EARTHWORM, *LUMBRICUS TERRESTRIS*

Our common large earthworm known also as angleworm and nightcrawler reaches a length of from 20 to 30 centimeters (8 to 12 inches) (Fig. 22:1). It is a long slender worm which is easily distinguished from one of the Nemathelminthes by the segments or metameres into which its body is divided. The division into metameres is made evident externally by grooves encircling the body. The adult earthworm is composed of approximately 150 segments. One end, which is the more pointed and usually in front when the worm crawls, is recognized as the **anterior** end; the other end which is blunter and flattened dorsoventrally is the **posterior** end. At the anterior end is the mouth. Projecting over the mouth is a lobelike structure, the **prostomium,** which resembles a metamere in being separated by a groove from the rest of the body. It is not, however, regarded as a metamere, since it lacks most of the organs usually present in a metamere. At the posterior end is the anus. The dorsal surface of the body is rounded while the **ventral surface** is more flattened and possesses in each metamere four pairs of small toothlike projections, the **setae.** If the earthworm is drawn through the fingers these setae give to the under side a rough, scrapy feeling. The setae enable the earthworm to retain a firm hold in its burrow and to resist being pulled out of it. In mature earthworms the region of the body extending from the thirty-first or thirty-second to the thirty-seventh metamere is swollen. This saddle-shaped swelling, called the **clitellum,** is due to the presence of glands which secrete material utilized in forming a cocoon in which the eggs are laid. The external surface of the body is covered with a thin transparent cuticle. Each metamere beyond the eighth bears

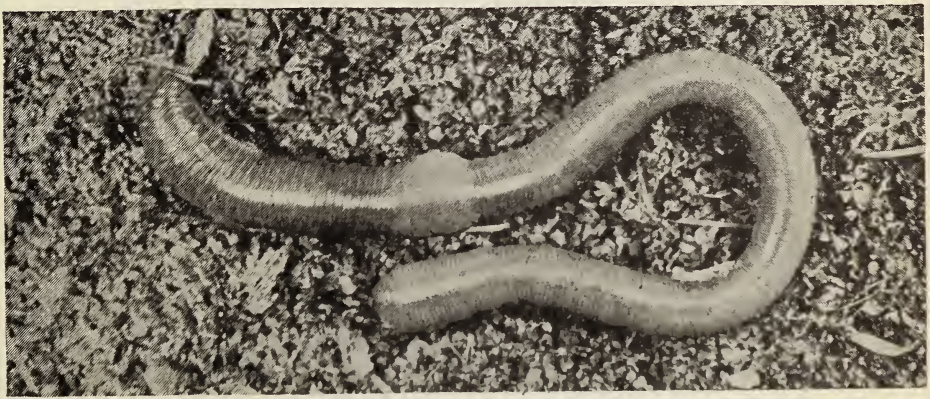

Fig. 22:1 An earthworm (*Lumbricus terrestris*, phylum Annelida, class Chaetopoda, order Oligochaeta). Photograph by J. W. Mavor.

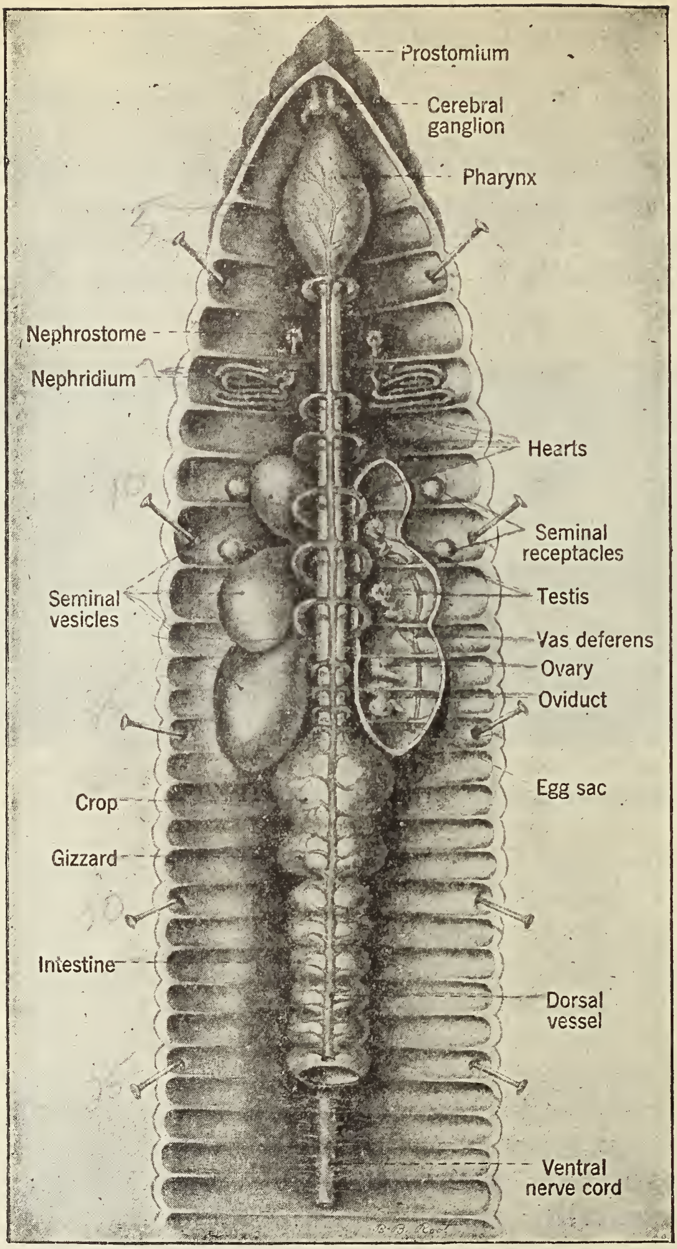

Fig. 22:2 An earthworm dissected from the dorsal side to show the internal organs. The pins are inserted at intervals of five metameres. The supraesophageal or cerebral ganglia usually lie in metamere III; the pharynx in metameres IV and V; and the hearts in metamere VII to XI. The structures labeled "testes" are sperm funnels; no testes are shown. The seminal vesicles on the right side of the illustration are cut away so as to reveal the ovary and oviduct which lie beneath them. The nephridia of only one metamere are shown. Nephridia occur in all of the metameres except the first three and the last. Drawn by B. B. Root, from Hegner, *College Zoology*, The Macmillan Company.

on its dorsal side near the next anterior metamere a minute pore by means of which the coelom communicates with the exterior. A number of other external openings occur, which, however, can be best considered in connection with the organs with which they connect.

If the body of an earthworm is slit open by cutting it lengthwise, it will be found, like that of *Ascaris*, to contain a cavity, which likewise surrounds a digestive tract extending the length of the animal (Fig. 22:2). The earthworm is, therefore, like *Ascaris* in possessing the **tube-within-a-tube type of body structure,** but its body cavity is a true coelom. The **coelom** of the earthworm is completely lined by mesoderm, into it open the excretory organs, and from its walls arise the germ cells. The coelom provides space for a number of organs which project into it, such as the nephridia, blood vessels, and nerve cord. Due to the presence of the coelom and its contained coelomic fluid, the digestive tract, blood vessels, and to some extent the nephridia are able to contract and expand independently of the other parts of the body, a freedom which they would not enjoy were space occupied by solid tissue. There is evidence that the coelom serves to some extent for the transport of food substances and waste products. The coelom is divided transversely by thin partitions, called **septa,** extending from the body wall to the digestive tract. The attachments of the septa correspond to the grooves on the surface of the body. The coelom is thus divided into compartments corresponding to the metameres. Small openings occur in the septa so that when a portion of the earthworm contracts, coelomic fluid flows from the coelom of the contracting metameres into the coelom of the adjacent metameres. The tube-within-a-tube plan of structure of the earthworm is well shown in a transverse section (Fig. 22:3). The body wall which forms the outer tube appears as the outer ring in the section. This is separated by a space, the coelom, from the inner tube, the intestine, represented in the section by the inner ring. We will now turn to a more detailed study of the separate organ systems or parts of the earthworm and will begin with the body wall.

The thin transparent cuticle already referred to covers the body externally. Under this is the **epidermis,** a layer of epithelial cells covering the body, which secrete the cuticle. In the epidermis are gland cells which secrete the mucus with which the body of the worm is usually covered and nerve cells which are sensitive to light, heat, and cold, chemical changes and mechanical contacts, and which send nerve impulses to the central nervous system.

Within the epidermis, and forming with it the body wall, are the circular and longitudinal muscles. The **circular muscles** form the outer layer immediately underlying the epidermis. The muscle fibers of these muscles run with their axes in the plane of the section; their contraction in any region of the worm tends to reduce its diameter. Within the circular muscles is a much thicker layer of **longitudinal muscles.** The muscle fibers of these muscles are cut across in the section since they run lengthwise in the worm. The contraction of the longitudinal muscles tends to shorten the worm in the region in which the contraction occurs. The layers of circular and longitudinal muscles are interrupted where the setae occur and at various external openings. The setae are small, toothlike structures which are arranged in pairs, there being four pairs, or eight setae, in each metamere. Two of these pairs are ventral and two

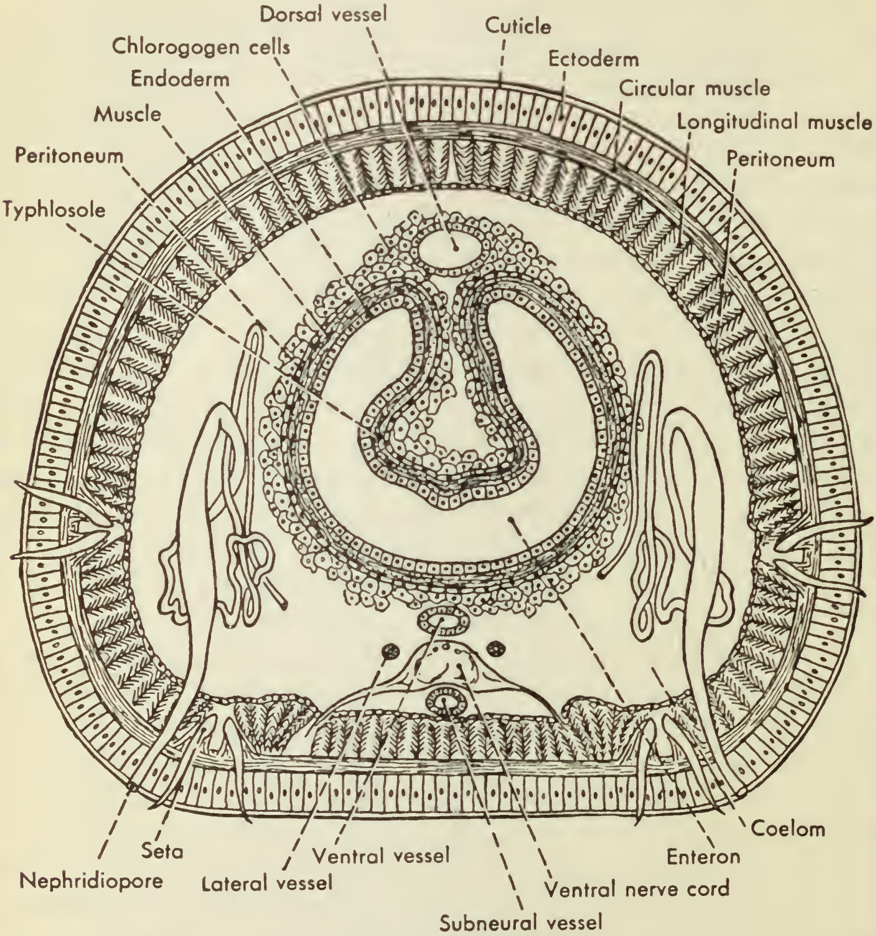

Fig. 22:3 Diagram of a cross section of an earthworm with the cell layers emphasized. The epidermis, intestinal epithelium, and the intestinal cavity have been labeled respectively — ectoderm, endoderm, and enteron. From Hegner, *College Zoology*, The Macmillan Company.

lateral. The setae are actuated by muscles and can be either protruded or retracted.

In connection with the structure of the body wall the method of locomotion of the earthworm may be advantageously studied. Let us consider what happens when the worm crawls forward. First the anterior end is moved forward. This is done by the contraction of the circular muscles in this region. The coelomic fluid and the tissues of the body of the earthworm, like those of any organism, are practically incompressible. When, therefore, the contraction of the circular muscles decreases the thickness of the body, it must increase its length. After this preliminary elongation of the body the anterior end is anchored by the setae, and a posterior portion is drawn up by the contraction of the longitudinal muscles. The portion drawn up is then anchored as was the anterior portion, and a more posterior portion is drawn up. The process continues until the entire length of the worm has been moved forward. In going into, or coming out of, its burrow, the worm uses a similar method, excepting that the body is anchored in the burrow by an annular thickening of the body.

The **digestive system** of the earthworm begins at the mouth which leads into a muscular **pharynx.** The muscles of the pharynx extend from its wall radially to the body wall. Their contraction enlarges the cavity of the pharynx and produces a suction by which food is taken in. This food consists of pieces of animal and vegetable matter which the earthworm collects at night and of soil which it passes through its digestive tract in making its burrow.

Following the pharynx is the **esophagus,** a thin-walled tube, extending almost to the fifteenth segment. On either side of the esophagus are **calciferous glands** which secrete calcium carbonate into the esophagus. The calcium carbonate probably serves to neutralize acid materials which may be taken in with the food. Beyond the fifteenth segment the digestive tract is enlarged into a thin-walled **crop** in which food is stored. Immediately posterior to the crop is the **gizzard,** a thick-walled muscular pouch in which the food material is ground up into fine particles. The grinding process is helped by the presence of grains of sand and other hard objects ingested with the food. The gizzard leads into the long, thin-walled **intestine** in which digestion and absorption occur. **Digestion** in the earthworm is probably very similar to that in a higher animal, the carbohydrates, fats, and proteins being acted on by enzymes secreted by cells in the wall of the intestine. Absorption occurs through the wall of the intestine. The absorbing and secreting surface of the intestine is increased by a dorsal infolding of its wall to form a structure called the

typhlosole. This appears, in the transverse section (Fig. 22:3), as a dorsal projection into the cavity of the intestine. Covering the outer surface of the intestine, and forming a mass in the typhlosole are peculiar yellowish cells called **chloragogen cells.** The exact function of these cells is not known but is probably excretory. The undigested material, of which there is an abundance, is passed out through the anus and forms the "castings" seen on lawns and other places where earthworms abound.

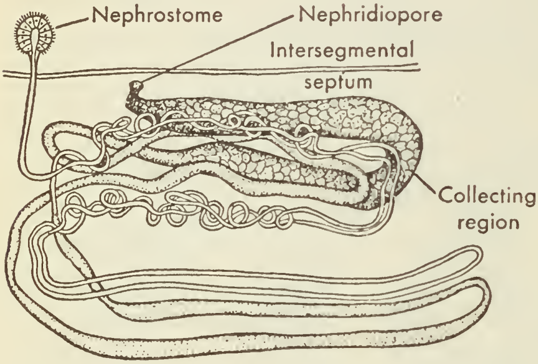

Fig. 22:4 Diagram of a nephridium of an earthworm. When in the body of the earthworm the nephridium is invested with soft tissue and the loops of the tubule are crowded together. From Wolcott, *Animal Biology*, McGraw-Hill Book Company, Inc.

Each of the metameres, excepting the first three and the last, has its own pair of excretory organs, or **nephridia** (Fig. 22:4). These organs will be considered in some detail because they are of a type which is first encountered here and which occurs in many animals and because they probably are similar to the primitive type of structure from which the kidneys of the higher animals have been evolved. A nephridium consists essentially of a coiled tube, opening on the one hand into the coelom by an opening called the **nephrostome,** and on the other hand to the exterior. The nephridia of the earthworm occur in pairs, one on either side of the intestine (Fig. 22:3) attached to the septa. The nephrostomes open into the coelom in one metamere, and the **nephridiopores** to the exterior in the metamere posterior to it. Glands in the walls of the nephridial tubes excrete waste products into the cavities of the tubes, and cilia on their walls cause an outward flow of coelomic fluid. The fluid flowing out through the nephridia carries the waste products to the exterior.

On account of its size and rather complicated structure the earthworm requires a circulatory system to carry nutrient material from the walls of the digestive tract to the various parts of the body, waste materials from the various parts of the body to the nephridia, oxygen from the skin to the tissues, and carbon dioxide from the tissues to the skin. The earthworm is the first of the lower animals in which we have encountered a vascular system. The **blood** of the earthworm consists of a **plasma** in which colorless corpuscles float. The red color of the blood is due to

hemoglobin dissolved in the plasma. The blood passes anteriorly along the length of the worm in a **dorsal blood vessel** which lies on the dorsal side of the intestine (Fig. 22:3). In the anterior region surrounding the esophagus are five pairs of muscular vessels called **aortic loops,** or **hearts** which force the blood from the dorsal vessel to a **ventral vessel** lying below the intestine (Fig. 22:5). In this vessel the blood passes, posteriorly, in the part behind the "hearts" and, anteriorly, in the part in front of the "hearts." From the ventral vessel the blood passes to the body wall, nephridia, and the ventral portion of the intestine. A single **subneural vessel** extends longitudinally ventral to the nerve cord and receives blood from the nerve cord and from the ventral body wall, and transmits it to **parietal vessels** arranged a pair to a segment, which also receive blood from the body wall and the nephridia. The blood from the parietal vessels passes into the dorsal blood vessel.

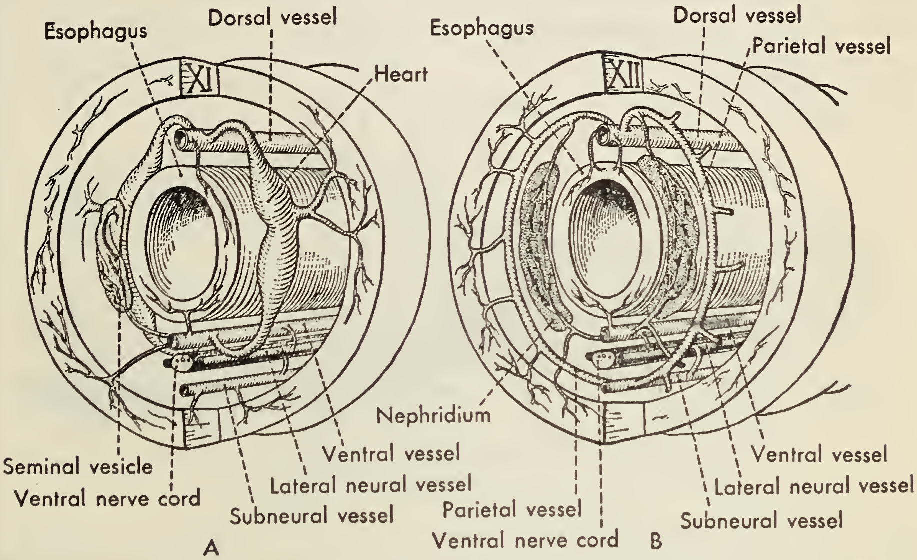

Fig. 22:5 Cross sections designed to show the circulation of the blood in the earthworm. A, the eleventh segment; B, the twelfth segment. From Hegner, *College Zoology*, The Macmillan Company.

In the **nervous system** of the earthworm most of the nerve cells are grouped together to form **ganglia.** Except in the first three metameres all of these ganglia occur in pairs in the ventral portion of the coelom between the digestive tract and the body wall, one pair to a metamere (Fig. 22:6). The two ganglia of the same metamere and the ganglia of successive metameres are connected by **nerve fibers** arising from their nerve cells, the whole structure forming a nerve cord. There are no ganglia in the first two metameres. In the third metamere, instead of being ventral, the ganglia are dorsal to the pharynx and form a pair of **suprapharyngeal ganglia** connected to the ventral nerve cord by **circumpharyngeal connectives.** From the ganglia nerve fibers extend to the various parts of the body. Some of these are **sensory fibers** arising from sensory nerve cells in the epidermis, while others are **motor fibers** arising in the ganglion cells of the nerve cord and branching in muscles. A nerve fiber contains protoplasm and is a process of a nerve cell comparable to a fine pseudopodium of an amoeba. A nerve cell with all its processes or nerve fibers is called a **neuron.** The term "neuron" is therefore equivalent to "nerve cell" but emphasizes the fact that the processes are included.

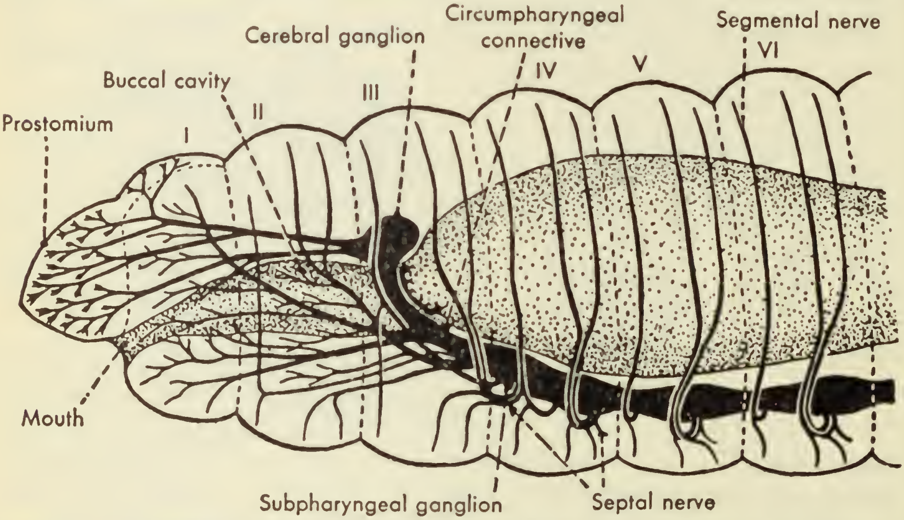

Fig. 22:6 Earthworm. Side view of anterior end showing the cerebral or suprapharyngeal ganglion, the subpharyngeal ganglia, and the larger nerves of one side. After Hess, from Hegner, *College Zoology*, The Macmillan Company.

When an earthworm is stimulated, let us say by being touched by a hard object, and moves away, this movement, due to the contraction of certain of its muscles, is the response to the stimulus. We can trace, in a general way, the path taken by the nervous impulse in such a reaction (Fig. 22:7). The stimulus is received by a **sensory nerve cell** located in the epidermis. A nerve fiber goes from this cell to a ventral ganglion where it ramifies, giving rise to numerous fine branches. The nerve impulse which is set up by the stimulus in the sensory nerve cell passes along the nerve fiber and out into its branches. From these latter it passes over to another set of fine branching nerve fibers which arise from a nerve cell located in the ventral ganglion and called a **motor nerve cell.** Besides the fine branches which put it into communication with the fibers of the sensory cell, the motor cell gives off a long fiber which ramifies in the muscles of the body wall, sending branches to muscle cells. The nerve impulse passes along this latter fiber and its branches and causes the muscle cells to contract. Exactly what the nervous impulse is will not be discussed at this time. The course which the nerve impulse takes in passing from the sensory cell to the muscle cell is called a **reflex arc.** In some cases the reflex arc is not so simple as that just described. A third nerve cell called in this case an **association neuron** may intervene between the fibers of the sensory and motor neurons. A nervous impulse originating in one or a few sense cells may be spread by association neurons to several metameres and cause many muscle cells to contract. The **sense organs** of the earthworm consist entirely of separate sense cells located in the epidermis. The earthworm is known to be sensitive to light, chemical substances, heat, and vibrations. Having no eyes it gets its information regarding the form and size of objects from the sense of touch.

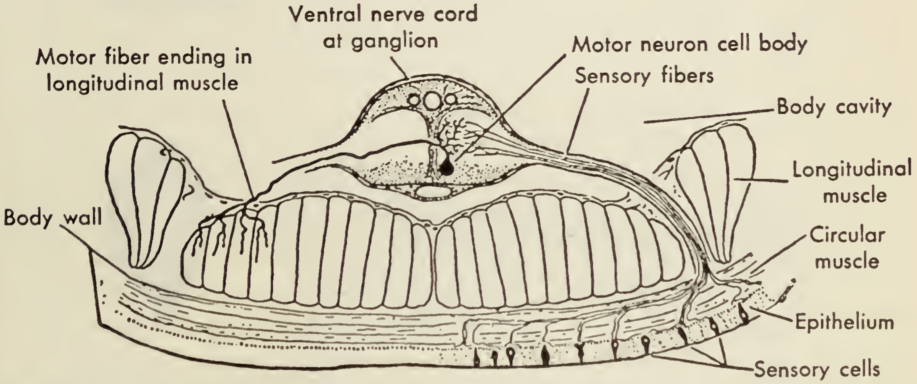

Fig. 22:7 Diagram of a portion of a cross section of an earthworm, showing the structures involved in a reflex arc. The epithelium is that of the epidermis. After G. H. Parker.

It will be well at this point to review the **metamerism** of the earthworm. Each metamere has been found to contain a portion, at least, of each of the following organs, or systems of organs: epidermis, circular and longitudinal muscles, coelom, nephridia, digestive tract, nerve ganglia, nerve fibers, sense cells — in fact all the organs necessary to carry on its individual life.

In contrast to the other organ systems, the reproductive organs are restricted to certain metameres in the anterior portion of the worm (Fig. 22:2). The earthworm is hermaphroditic. The **ovaries** are a pair of minute conical bodies lying in the coelom of the thirteenth metamere, each attached by a short stalk to the posterior surface of the septum separating metameres twelve and thirteen on either side of the nerve cord. The eggs are discharged by the ovary into the coelom. Ciliated funnels, one opposite each of the corresponding ovaries and attached to the anterior surface of the septum separating metameres thirteen and fourteen, carry the eggs from the coelom into the **oviducts.** The latter pass through the septum into segment fourteen where, after enlarging to form egg sacs, they pass through the body wall to open to the exterior by minute openings in the same segment. The female reproductive organs include two pairs of **seminal receptacles,** small saclike structures, in the ninth and tenth segments. These communicate with the exterior through openings on the ventral surface, between the ninth and tenth, and tenth and eleventh metameres, respectively, and receive spermatozoa from another worm (Fig. 22:2).

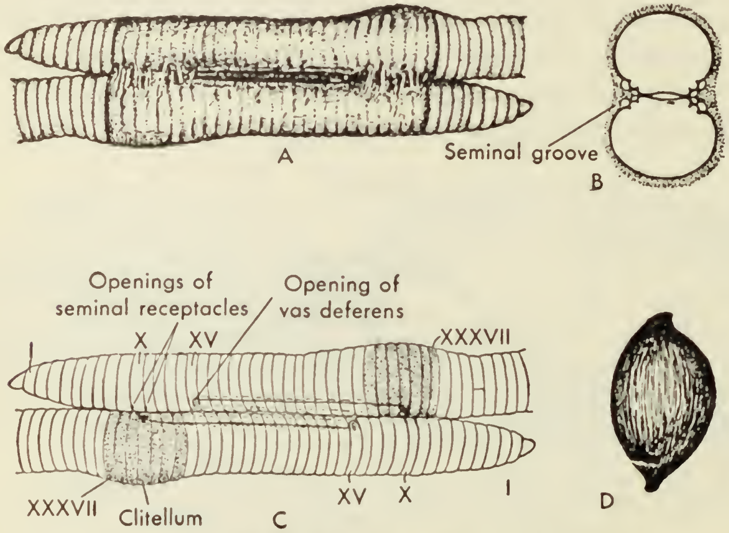

Fig. 22:8 Reproduction in the earthworm. A, two individuals enclosed in bands of mucus. B, transverse section showing seminal grooves. C, the path of the seminal fluid from the openings of the vasa deferentia of one worm to the openings of the seminal receptacles of the other. D, cocoon containing fertilized eggs. From R. H. Wolcott, *Animal Biology*, McGraw-Hill Book Company, Inc.

The **testes** lie in the tenth and eleventh metameres in a position corresponding to that in which the ovaries lie in the thirteenth metamere. They are enclosed in saclike **seminal vesicles** which bulge into the coelom of the ninth to the twelfth metameres. The cavities of the seminal vesicles are parts of the coelom separated from the main coelom in development. In the tenth and eleventh metameres, where the seminal vesicles of opposite sides are continuous, pairs of funnel-shaped openings lead from the seminal vesicles to pairs of **vasa deferentia** (singular, **vas deferens,** L. *vas*, a vessel, *deferens*, carrying down). On each side of the worm the two vasa deferentia of the same side join to form a single tube which passes posteriorly to open to the exterior by a pore in the fifteenth metamere (Fig. 22:2).

Although the earthworm is hermaphroditic, self-fertilization rarely, if ever, occurs, the eggs of one worm being fertilized by the sperm from another worm. This is made possible through the process of **copulation** (Fig. 22:8). When this occurs the two worms come together so that their anterior ends point in opposite directions, their ventral surfaces are in contact, and the clitellum of one worm is opposite the ninth and tenth metameres of the other. The adhering portions of the two worms come to be enclosed in a slime tube formed from mucus secreted by the worms. Grooves on the ventral surfaces of the worms conduct the sperms of one to the seminal receptacles of the other and vice versa. In this way, while one worm is passing its sperms into the seminal receptacles of another worm, it is simultaneously receiving sperms from the other worm into its own seminal receptacles. After copulation the earthworms separate and carry with them portions of the slime tube. A tubular **cocoon** is formed by each worm inside its portion of the slime tube from a horny substance secreted by the clitellum and passed forward over the body of the worm. As this cocoon passes the openings of the oviducts (metamere fourteen) eggs are laid into it; as it passes metameres ten and nine the spermatozoa received from the other worm are passed into it from the spermathecae and fertilize the eggs. In the cocoon the eggs develop into young embryo worms which escape and burrow into the ground.

Earthworms perform a useful and important work in the soil. They occur in all parts of the world except the extreme arctic and antarctic regions and desert lands. What they lack in size they make up for in numbers. It has been estimated that there are twenty-seven thousand of them in an acre of a grain field and about twice that number in an acre of garden soil. They are constantly taking the under soil from below the roots of plants and spreading it on the surface. Their castings are familiar evidence of their burrowing activity. In this way in time large quantities of soil are transferred. Charles Darwin, better known as the author of the *Origin of Species* and advocate of the theory of evolution, studied the activities of earthworms and wrote a book entitled *The Formation of Vegetable Mould through the Action of Worms.* He found that under favorable conditions earthworms could form new mold on the surface at the rate of 1 inch in thickness in 5 to 10 years.

The importance of earthworms for the fertility of the soil and the growth of plants is easily seen. Darwin expressed it by saying that "the plough is one of the most ancient and valuable of man's inventions, but long before he existed the land was in fact regularly ploughed and continues to be thus ploughed by earthworms." In moving the soil from deeper layers to the surface, not only do earthworms break it up and mix it with organic matter, but they also by their burrows provide easy access for air and water.

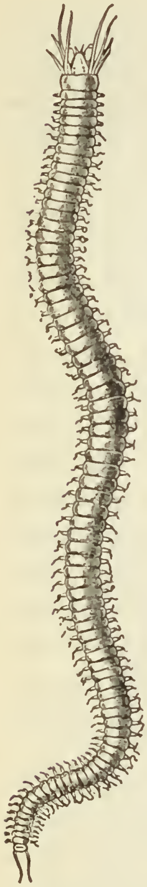

Fig. 22:9 A polychaete worm, *Nereis*. After Oersted, from Shipley and MacBride, The Cambridge University Press.

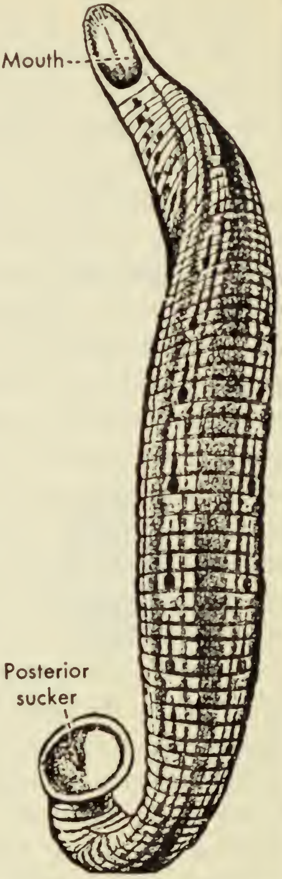

Fig. 22:10 *Hirudo medicinalis*, a leech. After Shipley and MacBride, from Hegner, *College Zoology*, The Macmillan Company.

2. OTHER ANNELIDS

The annelids are abundant and widely distributed. The earthworm is somewhat exceptional in being a land animal as most of the members of the phylum are aquatic. Other land forms are the manure worms (genus *Eisenia*) and the small white worms (*Enchytraeus albidus*) often used to feed small animals in aquaria and terraria. All of these belong to the order Oligochaeta of the class Chaetopoda, most of the members of which occur in fresh water. Some of these are quite small like the little *Nais* often found among algae collected from ponds. *Tubifex* is a common form which lives on the muddy bottoms of ponds. It forms a tube in the mud from which the hind end of its reddish body protrudes and waves about.

The members of Polychaeta (Fig. 3:19), the other order into which the Chaetopoda are divided, are almost exclusively marine. They show great variety of size, structure, and modes of life. Many are found in burrows in mud or sand flats as for example the clamworm, *Nereis* (Fig. 22:9). Others like the "sea mouse," *Aphrodite*, crawl over the bottom. Still others spend their lives swimming near the surface of the sea. Like the earthworm they provide food for larger animals.

The leeches (Fig. 22:10), class Hirudinea, are a rather uniform and specialized group living on the blood of other animals in the sea, fresh water, and on land.

3. THE PLAN OF STRUCTURE AND THE CHARACTERISTICS OF THE PHYLUM ANNELIDA

The **tube-within-a-tube plan of structure** is perfected in the Annelida to the extent that the coelom, now a true coelom, is lined throughout with mesoderm. To the tube-within-a-tube plan has been added metamerism, which consists in the transverse division of the body into a number of metameres which are similar and possess the more essential vegetative organs. A distinction is to be made between metamerism and strobilization as seen in the Scyphozoa and Cestoda. In metamerism the metameres develop simultaneously and remain together forming the body of an individual, while in strobilization the medusae, or proglottids, are formed as a succession of buds at one end of the strobila, or scolex, and reach maturity at different times.

An entirely new type of excretory organ, the **nephridium,** appears in the Annelida. A nephridium is typically an elongated tube with excretory gland cells and cilia in its wall, opening at one end into the coelom and at the other either directly to the exterior or indirectly through a duct.

Increased size and complication of structure have led to the development of a **circulatory system** consisting of blood vessels, some of which have muscular walls and pump the blood to the various parts of the body.

This same increase in size and complication has brought about the centralization of the nerve cells to form ganglia which are connected to form a **ventral nerve cord.**

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1. The earthworm, *Lumbricus terrestris* 427
2. Other annelids 438
3. The plan of structure and the characteristics of the Phylum Annelida 439

Questions

1. Define the terms coelom and metamerism.
2. Explain in detail how the earthworm is built on the tube-within-a-tube plan.
3. Describe the locomotion of the earthworm from the point of view of the muscles involved.

4. Describe the digestive system of the earthworm. Can you account for its relatively large size?
5. Describe a nephridium. What is its function?
6. Describe the circulatory system of the earthworm. What is the advantage of such a system in the earthworm?
7. Describe the nervous system of the earthworm.
8. Trace the path of a reflex.
9. What forms of stimuli is an earthworm adapted to receive?
10. Discuss in detail the structure and functions of the reproductive organs of the earthworm. How is cross-fertilization ensured?
11. Discuss briefly the plan of structure of the earthworm. How does it differ from that of a planarian?

Suggestions for Further Reading

Hegner, Robert W., *Invertebrate Zoology*, The Macmillan Company, New York, 1933, Chap. VIII.

Buchsbaum, Ralph, *Animals without Backbones*, The University of Chicago Press, Chicago, 1938, Chaps. 19 and 20.

Darwin, Charles, *The Formation of Vegetable Mould through the Action of Worms*, John Murray, London, 1881.

CHAPTER 23

The Arthropods — Cephalization — Jointed Appendages (Phylum Arthropoda)[1]

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1. GENERAL DISCUSSION

There are more known species of arthropods than of all the other known species of plants and animals combined. It can be said that roughly of the somewhat less than a million known species of organisms, more than half, i.e., about six hundred thousand, are arthropods while the rest are about equally divided between the other animals and plants. The phylum includes lobsters, crayfish, centipedes, millipedes, insects, and spiders.

To the structural advances shown in the annelids, tube-within-a-tube body, metamerism, and organ systems, the arthropods have made two important additions. Although the word "head" has been used in describing the members of some of the phyla previously considered, in no case is there a sharp differentiation of the body into different parts. In the phylum Arthropoda this differentiation of the body takes place; certain of the most anterior metameres have become differentiated into a head, and in the more specialized members of the group a thorax and an abdomen. Not only is the body divided in this way, but the sense organs come to be located in the head and the nervous system is larger and more highly developed in the anterior than in more posterior metameres. Thus the control of the body comes to be more and more located in the anterior portion. This evolutionary tendency, which reaches its greatest development in the vertebrates and man in particular, is called **cephalization** (Gr. *cephalon*, head). The second contribution of the arthropods is found in the development of **jointed appendages.** It is this characteristic which has given the name to the phylum (Gr. *arthros*, a joint + *pous*, a foot). The development of this type of appendage is made possible in the arthropods by the development over the entire surface of the body of a hard chitinous **exoskeleton** which is thin and flexible where the joints occur.

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[1] The sections dealing with the crayfish, grasshopper, and bee are independent so that any one or two may be omitted, according to the judgment of the instructor, without seriously interrupting the continuity of the text.

The exoskeleton is composed of a substance called **chitin** which is secreted by the outer cellular layer of the skin, called, in arthropods, the **hypodermis.** What appear to be solid plates or processes projecting from the surface of the body are in reality folds or outpocketings of the hypodermis covered with chitin. The fine hairs which occur in certain species are formed by special cells of the hypodermis. Where joints occur the exoskeleton is thin, elastic, and usually folded to allow movement.

The phylum Arthropoda is divided into five classes. We will refer to only three of these.

The class **Crustacea** includes lobsters, crayfish, shrimps, crabs, barnacles, and the extinct trilobites. Nearly all of them are aquatic animals and breathe by means of gills.

The class **Insecta** includes all the many kinds of insects such as cockroaches, grasshoppers, dragonflies, houseflies, butterflies, moths, beetles, bees, and ants. In insects the body is divided into head, thorax, and abdomen. The thorax bears three pairs of legs and frequently also two pairs of wings. The abdomen is without paired appendages except a pair of ovipositors, or egg placers, in the female. Insects are land animals and breathe air, but many species live in water during the early (larval) part of their lives.

The class **Arachnida** includes spiders, daddy longlegs, scorpions, mites, ticks, an interesting "living fossil" known as the king crab, and the extinct eurypterids, scorpionlike creatures which reached a length of 5 feet. Arachnids can usually be easily distinguished from insects, which form the previous group, by the fact that most of them have eight legs (four pairs).

2. TYPES OF ARTHROPODS

A. THE CRAYFISH

The crayfish, sometimes referred to as crawfish, is a near relative of the more familiar lobster, but while lobsters live in the sea, the crayfish is a fresh-water animal, living in small streams and along the shores of ponds. It usually remains hidden during the day but is active at night. The common American crayfishes belong to the genus Cambarus.

(1) EXTERNAL FEATURES AND APPENDAGES

The body of a crayfish or lobster (Fig. 23:1) is readily seen to be divided about the middle into an anterior portion called the **cephalo-**

thorax (Gr. *cephalon*, head + *thorax*, chest), and a posterior portion called the abdomen. A closer inspection of the abdomen shows it to be divided into six ringlike segments somewhat similar to the metameres of the earthworm. The segments of the abdomen are indeed true metameres as will later be clear from a study of their external and internal structure. The cephalothorax is composed of a head and thorax which have become secondarily fused into one; the more primitive relatives of the crayfish have the head and thorax separated. The metamerism of the cephalothorax is masked by the development of a rigid shell or **carapace** which covers it dorsally and at the side. The exoskeleton conforms closely

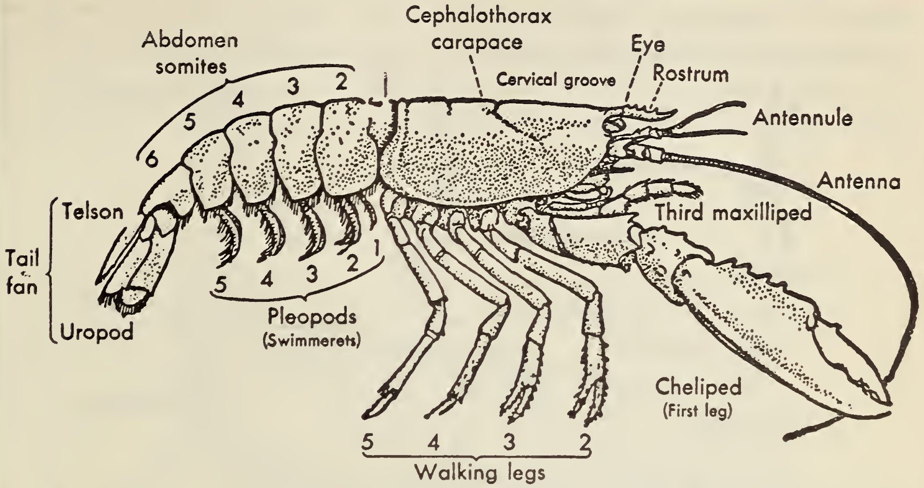

Fig. 23:1 External features of a lobster. After Calman, from Hegner, *College Zoology*, The Macmillan Company.

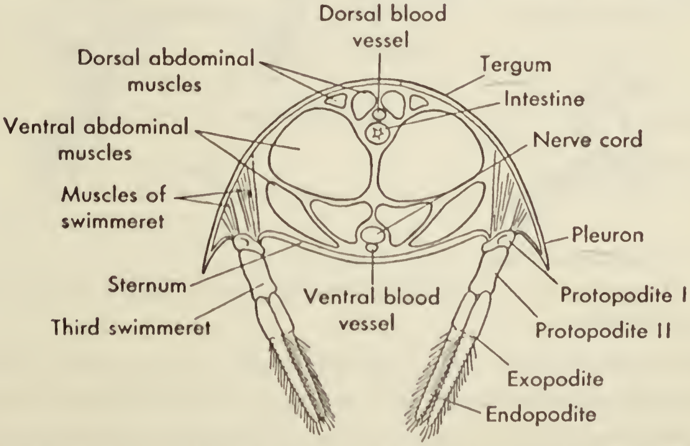

Fig. 23:2 A cross section of the abdomen of a crayfish cut between the second and third abdominal segments, showing the third pair of abdominal appendages.

to the shape of the body and protects and supports the soft parts. At the joints it is thin and flexible. The relation of the exoskeleton to the other parts of the body is well seen in a cross section of the abdomen passing through a metamere (Fig. 23:2). The dorsal portion called the **tergum** is convex and is continuous at each side with a projecting fold called the **pleuron** (plural, *pleura*). The covering of the ventral side, which is flattened, is called the **sternum**. The sternum is transparent, flexible, and thinner than the tergum or pleura. The appendages are attached laterally on either side of the sternum.

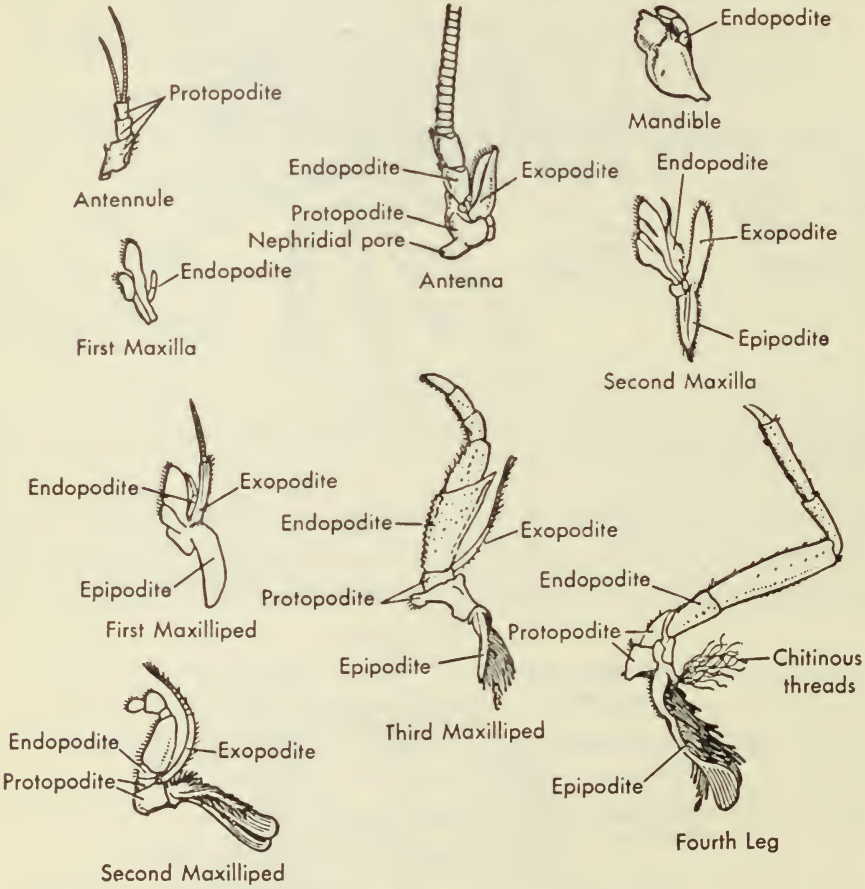

Fig. 23:3 Appendages of a crayfish. After Kerr, from Hegner, *College Zoology*, The Macmillan Company.

The body consists of nineteen metameres, thirteen in the cephalothorax and six in the abdomen. Each metamere bears a pair of appendages. Since the differentiation of the metameres and of the appendages takes place from anterior to posterior, the more highly differentiated structures being anterior, the appendages showing the most primitive and simplest plan of structure are those borne on the abdominal segments. We will begin our study with a typical abdominal appendage. Such an appendage (Fig. 23:2) consists of a short, straight part divided transversely into two segments called a **protopodite,** and two flat, flaplike portions, each movably attached to the protopodite. The outer of these flat portions is called the **exopodite,** and the inner the **endopodite.** The plan of structure shown in the abdominal appendages and called **biramous** (L. *bi*, two + *ramus*, a branch) is found in a more or less modified form in the other appendages of the crayfish.

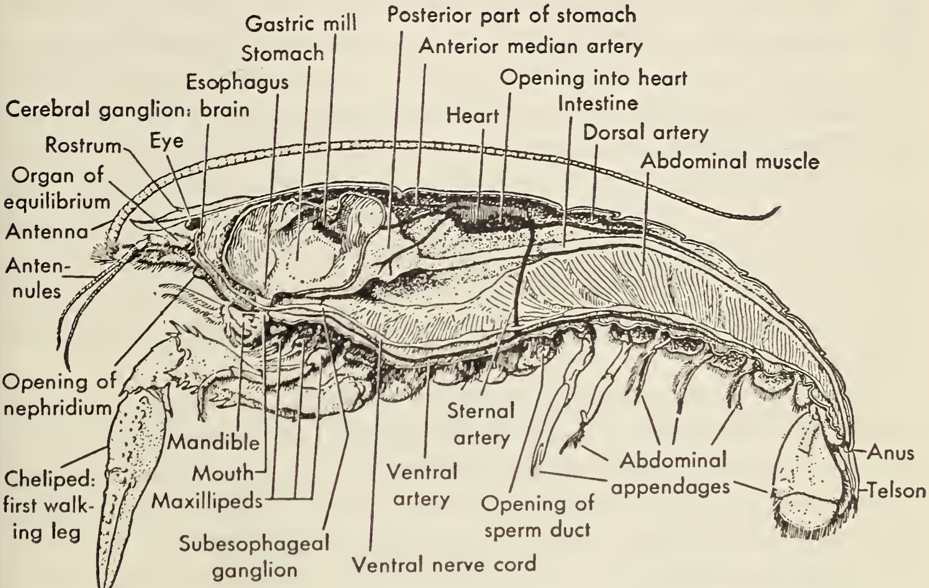

Fig. 23:4 Crayfish, *Cambarus affinis*, male. Dissection, lateral view. Cerebral ganglion is equivalent to supraesophageal ganglion. From L. L. Woodruff, *Animal Biology*, The Macmillan Company.

The **eyes,** although stalked and movable, are not regarded as appendages because they do not show the typical biramous structure. The first and second pairs of appendages, called **antennules** and **antennae,** respectively, are organs of touch and taste. In an antennule (Fig. 23:3) the exopodite and endopodite each consist of many segments. Since the protopodite contains three segments there is some doubt whether the antennules are really comparable to the other appendages. This is not true of the antennae where the protopodites consist of two segments. The exopodite of the antenna is a flat, scalelike structure consisting of a single segment, while the endopodite is many jointed and nearly as long as the body.

The mouth of the crayfish opens on the under side of the head (Fig. 23:4), and the food is passed forward and upward to it from the under side of the thorax. Six pairs of appendages play the parts of knives, forks, and spoons. These appendages move from side to side, tearing and working the food toward the mouth. They consist of one pair of mandibles, two pairs of maxillae, and three pairs of maxillipeds. In describing them it is well to begin with the third maxillipeds. If the antennules are designated the first pair of appendages, then the third maxillipeds are the eighth pair (see table of appendages). The **third maxillipeds** (L. *maxilla*, jaw + *pes*, foot) are relatively large and possess well-developed protopodites, endopodites, and exopodites. The **second** and **first maxillipeds** are progressively smaller and more flattened. The **maxillae** are still smaller and more flattened than the maxillipeds. The mouth is guarded by the **mandibles** or jaws. It is interesting to note that in the crayfish the mandibles work from side to side instead of up and down as do our jaws; also in the crayfish the mandibles are outside the actual mouth opening and are really appendages or modified legs. The part of the appendage which acts as a jaw is the first segment of the protopodite. The second segment of the protopodite is small and supports a small endopodite or palp. The exopodite is absent.

The most conspicuous appendages of a crayfish or lobster are pairs numbered nine to thirteen called **walking legs.** The ninth pair which bear the pincers are also called **chelipeds,** from the Greek word *chela* meaning "claw" and the Latin word *pes* meaning "foot." In these appendages the exopodites, although present in the embryo, are absent in the adult. The pincers are formed by the last and next to the last segments of the endopodite, the end of the latter growing out to form a fixed jaw against which the last segment is movable.

The first two pairs of **abdominal appendages,** numbers fourteen and fifteen, take the form of copulatory organs in the male and come together to form a pair of tubes through which the sperm is passed to the seminal receptacles of the female; in the female these appendages are rudimentary. The third to fifth abdominal appendages, called **pleopods** or swimmerets, have the typical structure already described, and are used to create a current of water under the body and in the female serve also for the attachment of eggs during the breeding season. The last pair of abdominal appendages, number nineteen, are called **uropods** (Gr. *ura*, tail). In these the protopodite consists of one broad segment, the exopodite of an oval plate divided by a transverse groove and the endopodite of a similar but undivided plate. The uropods are used when the crayfish swims backward by bending its abdomen under its thorax. The abdomen ends in a flattened structure called the **telson** on the ventral surface of which is the anus. It is doubtful whether the telson represents a terminal metamere.

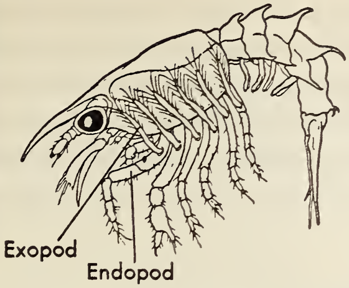

Fig. 23:5 Mysis stage of lobster. Redrawn from Calkins, *Biology*, after Herrick, by permission of Henry Holt and Company, Inc.

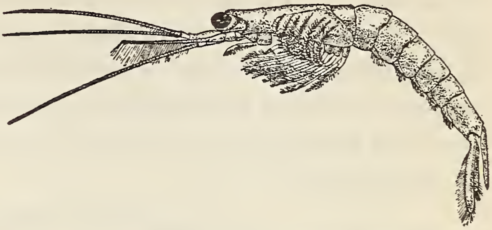

Fig. 23:6 Mysis (*Michtheimysis stenolepis*). A relative of the crayfish with biramous "walking legs." From Hegner, *College Zoology*, The Macmillan Company.

The structure of the appendages can be understood best after a study of their development in the young. The young lobster happens to be a

TABLE 23:1. APPENDAGES OF CRAYFISH

	NUMBER	NAME	SEGMENTS IN PROTOPODITE	SEGMENTS IN EXOPODITE	SEGMENTS IN ENDOPODITE	FUNCTION
Head	I	Antennule	3	Many	Many	Touch, taste, equilibration
	II	Antenna	2	1	Many	" " "
	III	Mandible	2	0	2	Crushing food
	IV	Maxilla	2	0	1	Passes food forward
	V	Maxilla	2	1	1	Makes current of water
Thorax	VI	Maxilliped	2	Many	2	Touch, taste, passes food
	VII	Maxilliped	2	Many	5	" " " "
	VIII	Maxilliped	2	Many	5	" " " "
	IX	Cheliped	2	0	5	Offense, defense
	X	Walking leg	2	0	5	Walking
	XI	Walking leg	2	0	5	"
	XII	Walking leg	2	0	5	"
	XIII	Walking leg	2	0	5	"
Abdomen	XIV	Pleopod				Reduced in ♀, copulation in ♂*
	XV	Pleopod				Reduced in ♀, copulation in ♂
	XVI	Pleopod	2	Many	Many	Movement of water, attachment of eggs in ♀
	XVII	Pleopod	2	Many	Many	Movement of water, attachment of eggs in ♀
	XVIII	Pleopod	2	Many	Many	Movement of water, attachment of eggs in ♀
	XIX	Uropod	1	1	1	Swimming

* The sign ♂ (bow and arrow) signifies male, while the sign ♀ (hand mirror) signifies female.

better object in which to study this development than the crayfish. It will be sufficient for our present purpose if we study a stage called the **mysis stage** (Fig. 23:5), so named because it resembles a small shrimplike animal named *Mysis* (Fig. 23:6). In the mysis stage all of the appendages, except the first pair or the antennules, show the structure of a typical biramous appendage, a protopodite consisting of two segments, an exopodite and an endopodite. In the later stages of development this structural plan becomes modified as already noted in the description of the appendages.

(2) INTERNAL STRUCTURE

The body of the crayfish, like that of the earthworm, shows a tube-within-a-tube structure, the exoskeleton, with its attached muscles forming the outer tube while the digestive tract, which is enlarged anteriorly forming the stomach, constitutes the inner tube (Fig. 23:4). The **true coelom** is much reduced and is represented in the adult only by the cavities of the gonads and excretory organs.

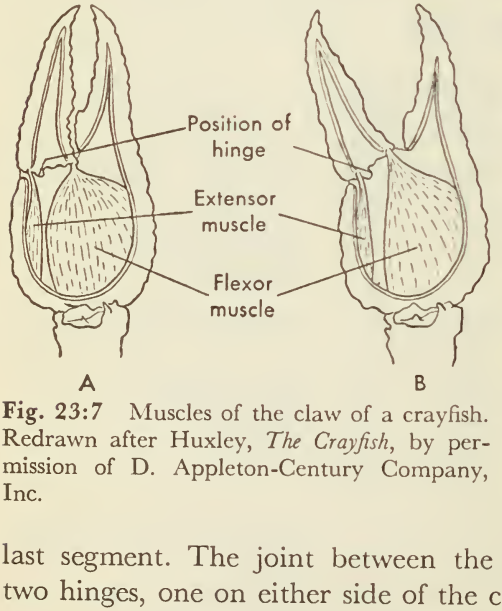

Fig. 23:7 Muscles of the claw of a crayfish. Redrawn after Huxley, *The Crayfish*, by permission of D. Appleton-Century Company, Inc.

The muscles of the crayfish move the parts of the exoskeleton. Their action is well illustrated in a claw (Fig. 23:7). As explained in discussing the appendages, the claw is formed by the last and next to the last segments of the appendage, a process growing out from the next to last segment and forming one of the jaws of the pincer while the other jaw is formed by the last segment. The joint between the two jaws thus formed contains two hinges, one on either side of the claw. These hinges keep the jaws moving in the same plane. Over the rest of the joint the exoskeleton is soft and flexible. Two muscles are responsible for the movements of the jaws, an extensor muscle and a flexor muscle. The **extensor muscle** opens the jaws. It is attached to, or **inserted** on, the exoskeleton near the base of the outer side of the last segment and to the exoskeleton of the corresponding side of the next to the last segment. This latter place of attachment may be called its **origin.** Since this muscle lies outside a line joining the two hinges it is easily seen that when the muscle contracts the jaw moves away from its partner, opening the pincer. The **flexor muscle** is much the larger and its action closes the jaws. It is attached, or inserted on, the inner side of the base of the exoskeleton of the last segment and to the side of the exoskeleton of the next to last segment. Since the line of action of this muscle lies inside the line joining the hinges, when it contracts the jaw closes on its fellow, a fact of which the unwary handler of these animals may become suddenly conscious.

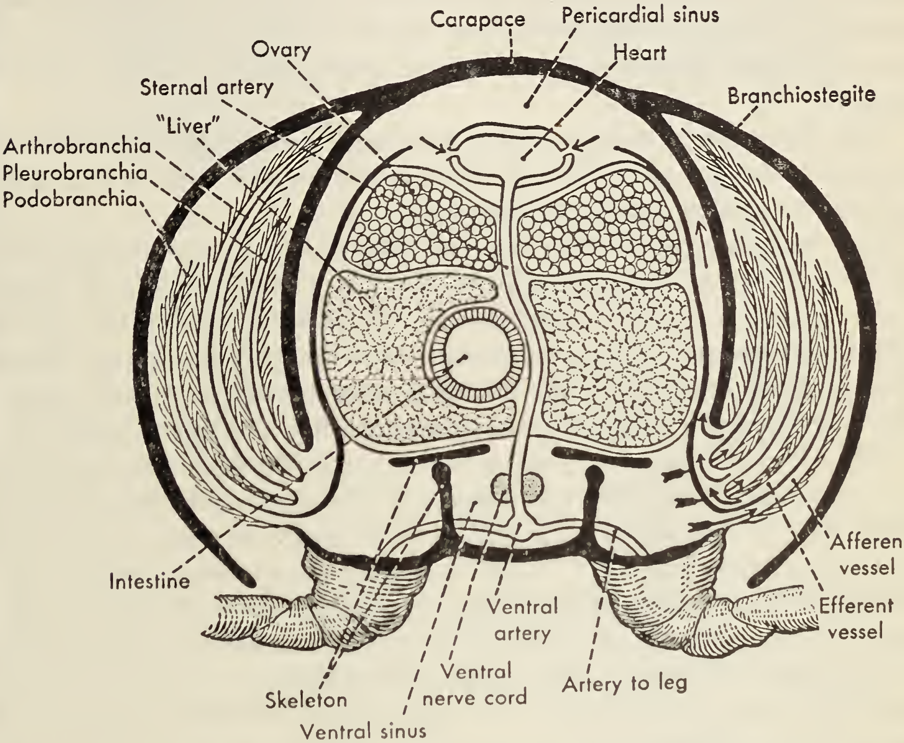

Fig. 23:8 Crayfish. Diagram of a cross section showing arrangement of the gills and some of the internal organs. From Hegner, *College Zoology*, The Macmillan Company.

The **digestive system** of the crayfish (Fig. 23:4) resembles that of the earthworm although differing from it in many details. A short esophagus leads from the mouth to a large stomach which is divided into three parts: an anterior part, the **cardiac portion,** an intermediate portion called the **gastric mill,** and a posterior part, the **pyloric portion.** The pyloric portion of the stomach is continuous with the long, fine intestine which opens to the exterior by the **anus.** A pair of **digestive glands** discharge their secretions into the anterior portion of the intestine. The chitinous covering of the body is folded in at the mouth and anus so that the stomach and all of the intestine except a short portion just posterior to the stomach, called the **mid-gut,** are lined with chitin. In the gastric mill this chitin is thickened to form three teeth which complete the tearing up of the food begun by the appendages. Absorption of digested food takes place only through the cells lining the mid-gut and the digestive glands. The food passes into the cavities of the digestive glands through their ducts.

The **respiratory system** of the crayfish consists of a series of plumelike external **gills** attached to certain of the thoracic appendages and concealed under the lateral folds of the carapace, which form a **gill chamber** on either side (Fig. 23:8). A current of water through the chamber and over the gills is kept up by a chitinous plate attached to the second maxilla.

The **excretory system** is limited to a single pair of organs resembling nephridia, located one at the base of each antenna and opening by a duct on the first segment of the protopodite.

The **vascular system** of the crayfish differs in many respects from that of the earthworm. In the first place it is not a closed system of vessels within which the blood is confined, for the blood goes from the arteries into **blood sinuses** which are merely spaces between the tissues. These blood sinuses constitute what is called a **hemocoel** or blood cavity. Secondly there is a definite pumping organ called the **heart** (Fig. 23:4).

The heart lies in a pericardial sinus in the thorax dorsal to the intestine. It contracts rhythmically and pumps the blood into **arteries,** of which there are a number, some taking blood to the head and thorax and others to the digestive glands and intestine. A large artery runs ventrally connecting with a ventral artery. From the arteries the blood goes to fine tubes called capillaries. The ends of the capillaries open into blood sinuses which return the blood to the pericardial sinus. On its way the blood passes into and out of sinuses in the gills where it receives oxygen and loses carbon dioxide.

Of all the organ systems of the crayfish, the nervous system and the sense organs show the greatest advance beyond those of the earthworm. Although the whole of the outer surface of the body is sensitive to touch and taste, the surface of the pincers has been found to be most sensitive to touch and the outer ramus (exopodite) of the antennules the most sensitive to taste. It seems that the crayfish is without any sense of hearing. The sense of equilibrium, which helps to enable the crayfish to maintain an upright position, is located in two small chitin-lined sacs contained in the basal segments of the antennules. Grains of sand rolling around in these sacs stimulate sensory hairs projecting from the wall. The sense of sight is well developed. The two **compound eyes** are at the ends of movable stalks and can be directed independently over a large field. Each compound eye is composed of approximately twenty-five hundred single eyes or **ommatidia** (Fig. 23:9). Each ommatidium resembles a minute telescope directed at a point in space. It does not give an individual picture but only a light or dark spot. The arrangement of these light or dark spots at the back of the crayfish's eye gives it a mosaic or patchwork picture of the field of vision. The picture which the crayfish sees is flat and the picture seen by one compound eye is different from that seen by the other unless, as seldom happens, both eyes are directed in the same direction. The eye of the crayfish would seem to be well adapted for the detection of moving objects.

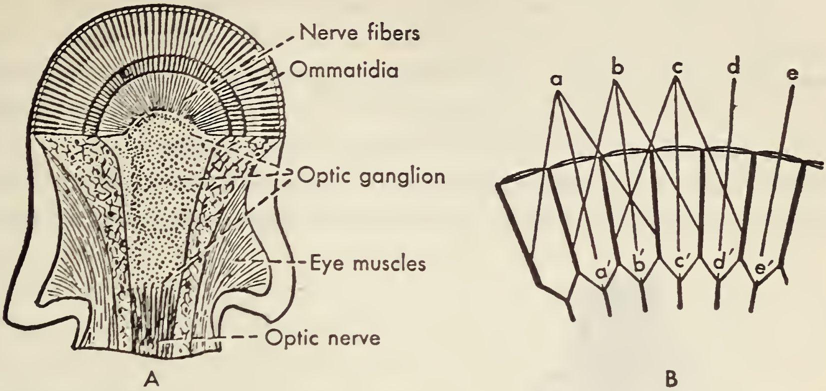

Fig. 23:9 Crayfish. A, eye in longitudinal section. B, diagram of part of a compound eye showing how rays of light are absorbed by the pigment surrounding the ommatidia and that only those that pass through the center such as *a-a′*, *b-b′*, etc., reach the nerve fibers. From Hegner, *College Zoology*, The Macmillan Company.

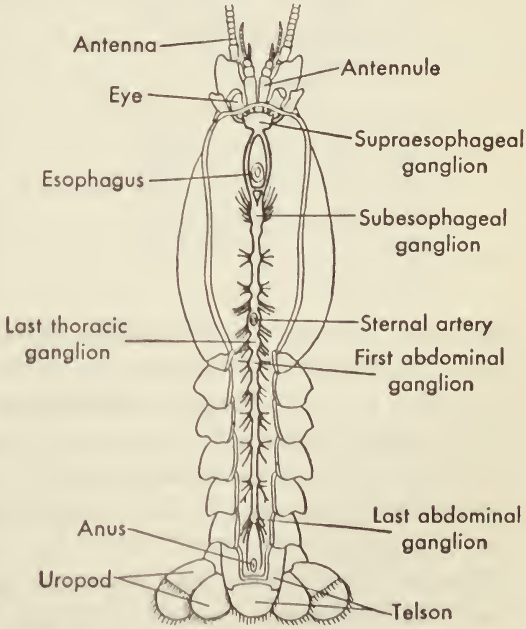

Fig. 23:10 Central nervous system of the crayfish (*Astacus fluviatilis*), viewed from above. After Huxley, *The Crayfish*, by permission of D. Appleton-Century Company, Inc.

The **central nervous system** of the crayfish is not unlike that of the earthworm but it conforms to the cephalization of the other organs of the animal's body (Fig. 23:10). In the embryo each of the nineteen metameres has its own pair of ganglia. In the adult, however, the two ganglia constituting a pair in each metamere are fused and certain fusions occur between the ganglia of different metameres. Thus the ganglia of the first and second metameres fuse to form a **supraesophageal ganglion** and the ganglia of the third to the seventh metameres fuse to form a large **subesophageal ganglion.** The other metameres have separate ganglia. From the supraesophageal ganglion nerves go to the antennules, antennae, and eyes and also to certain of the internal organs.

As the study of the external features has already shown, the sexes are separate in the crayfish. Both the ovaries and testes are paired, hollow organs containing cavities which are portions of the much-reduced coelom. The sperm are discharged into the cavity of the **testes** (Fig. 23:11) and pass out through **vasa deferentia** or sperm ducts opening on the first protopodites of the last pair of walking legs. The eggs are passed from the cavities of the **ovaries** (Fig. 23:12) to the exterior through **oviducts** which open on the first protopodite of the third pair of walking legs, counting the chelipeds.

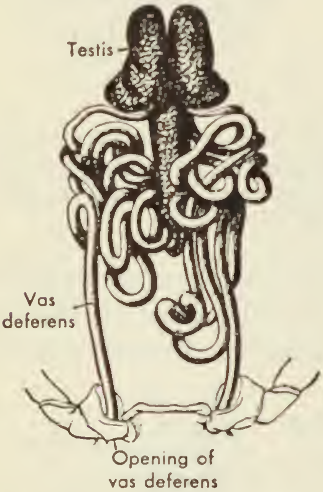

Fig. 23:11 The crayfish (*Astacus fluviatilis*). The male reproductive organs. After Huxley, *The Crayfish*, by permission of D. Appleton-Century Company, Inc.

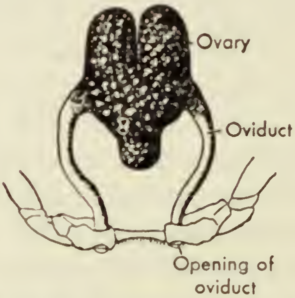

Fig. 23:12 The crayfish (*Astacus fluviatilis*). The female reproductive organs. After Huxley, *The Crayfish*, by permission of D. Appleton-Century Company, Inc.

The breeding season begins in the autumn when copulation takes place. Spermatozoa are transferred from the vasa deferentia of the male to the **seminal receptacles** of the female, by means of the first and second abdominal appendages which in the male are modified into copulatory organs. The seminal receptacles are cavities lined by chitin and situated between the fourth and fifth pairs of walking legs. It appears that the spermatozoa remain alive in the seminal receptacles until the following spring when the eggs are laid and fertilization occurs. The eggs adhere to the swimmerets of the female until hatched. The above description applies to *Cambarus.* Seminal receptacles are absent in some genera of crayfish.

The young hatch from the eggs as larvae, differing in a number of ways from the adult. About 24 hours after hatching the larvae shed their exoskeletons, a new one being then secreted by the hypodermis. The phenomenon of shedding the exoskeleton is called **ecdysis** or molting. It occurs about seven times during the first summer and at longer intervals during the life of the animal, which is about three years. Growth in size occurs in the short intervals between molting and the formation of a new exoskeleton.

(3) THE ECONOMIC IMPORTANCE OF THE CRUSTACEA

Crayfish are canned and eaten in the United States but their larger relatives, the lobsters, are of more economic importance.

Lobsters are caught in traps or pots, which consist of a coarse framework of laths in the shape of a box about 3 feet, 6 inches by 1 foot, 10 inches. The ends are of coarse netting with a round hole about 6 inches in diameter surrounded by a small hoop which is drawn into the trap and tied there. The lobsters crawl in through the hoop but usually do not find their way out. The traps are baited with fish and contain a stone to sink them to the bottom. They are set in shallow water in summer (10 to 30 feet) and in deeper water in winter (100 to 300 feet). Lobsters are usually kept alive in "crates" and shipped alive on ice to market. Lobsters are caught and used as food in Europe, but the greatest lobster fishery in the world is on the eastern coast of the United States and Canada.

Shrimps and prawns are caught either with wide hand nets with a straight edge which are pushed by hand along the sea bottom near shore or by "trawls" drawn by powerboats. The trawls are large nets in the shape of a huge bag with boards tied at an angle at either side. When pulled through the water the boards, known as otter boards, tend to separate and open out the net. There are extensive shrimp fisheries on the coasts of Florida and Louisiana where shrimp are canned.

Crabs are caught in traps like lobsters or on baited lines. No hooks are used. The line is pulled to the surface. The crabs follow the bait and are scooped up with a dip net. Soft-shelled crabs are merely ordinary or hard-shelled crabs just after they have molted. Since in this condition they are usually in hiding they must be sought for with a hand net.

B. THE GRASSHOPPER

(1) EXTERNAL FEATURES

There are a number of species of grasshoppers and locusts in the United States. The eggs of most American species are laid in late summer or autumn and hatch in the spring into wingless hoppers which undergo a gradual or "incomplete metamorphosis" into the adult form during the summer (Fig. 23:13).

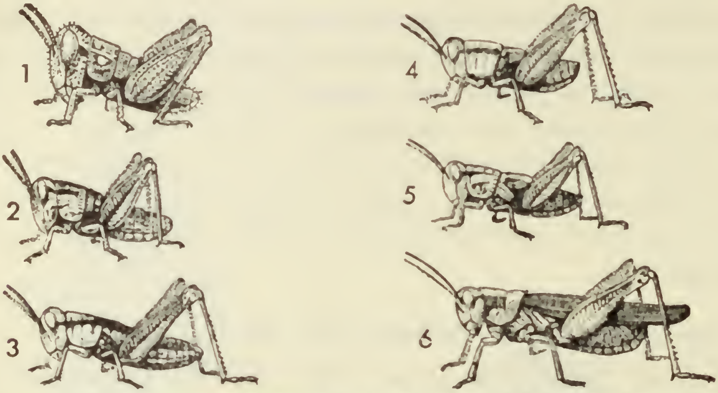

Fig. 23:13 Incomplete metamorphosis of a grasshopper (*Melanoplus femurrubrum*), showing five nymph stages, 1–5, and an adult or imago, 6. Note the change in proportions and the gradual growth of the wings. After Packard, from Hegner, *College Zoology*, The Macmillan Company.

As is the case in all insects the body is encased in a hard outer covering composed of a substance called **chitin** which is secreted by a layer of epithelial cells which, with the chitin, form the body wall. This covering of chitin constitutes the **exoskeleton**. In certain parts of the body joints occur where the exoskeleton is thin and flexible permitting movement.

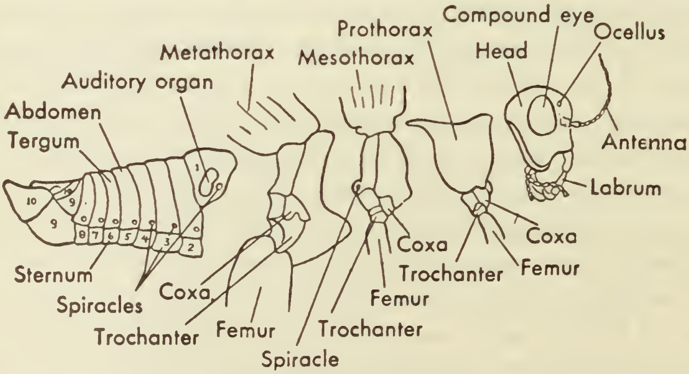

Fig. 23:14 Lateral view of exoskeleton of a grasshopper. 1–10, abdominal metameres. Redrawn after Packard, *A Textbook of Entomology*, The Macmillan Company.

The body is divided into **head, thorax,** and **abdomen** (Fig. 23:14). The abdomen and thorax are divided into segments or metameres, the thorax consisting of three metameres and the abdomen of ten. The head of the adult grasshopper is not divided into metameres. In the embryo, however, there is evidence of a primitive metamerism. Thus the body of the grasshopper, like that of the earthworm, is seen to be composed of metameres. However, there is not the close resemblance between the different metameres found in the earthworm. While the first eight metameres of the abdomen are very similar, those of the thorax are not only different from those of the abdomen but differ among themselves. Again, in the head the primitive metamerism is much modified, the separate metameres being no longer recognizable. The exoskeleton of a typical metamere, seen best in the abdomen, consists of a dorsal portion or **tergum** and a ventral portion or **sternum.**

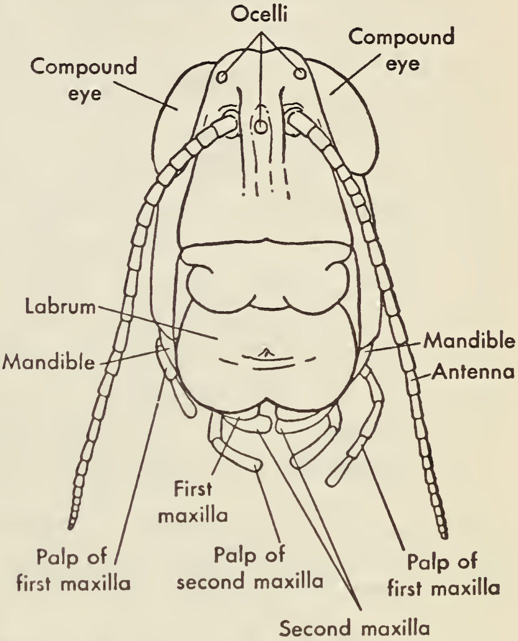

Fig. 23:15 Head of a grasshopper, front view.

On each side of the head are the large, oval, **compound eyes** (Fig. 23:15). These eyes are set into the head and covered by the chitinous exoskeleton which at this point is transparent. The eyes are not movable and in order to change the field of view the head must be moved. The structure of the eyes will be referred to in a later section. In front of the eyes are the first pair of appendages, the many jointed **antennae** or "feelers." On the ventral side of the head surrounding the mouth are the mouth parts (Fig. 23:16). In front of the mouth is an unpaired flap of chitin called the **labrum** or upper lip. This moves up and down as the insect eats. On either side of the mouth are the **mandibles** or jaws. The jaws of an insect differ from those of a mammal like ourselves in being in front of, or rather outside, the mouth and in working from side to side instead of up and down. Behind the mandibles, also on either side of the mouth, is the **first pair of maxillae,** each consisting of a jawlike portion and a palp. The **second pair of maxillae** are fused in the median line and form the **labium** or lower lip. Like the first maxillae each of these consists of a jawlike portion (which is fused with its mate) and a palp. Projecting from the floor of the mouth cavity and appearing between the upper lip or labrum and the lower lip or labium is a chitinous projection called the tongue or **hypopharynx.** Only the mandibles and the first and second maxillae are regarded as true jointed appendages. The food of the grasshopper consists chiefly of pieces of blades of grass and its mouth parts are adapted to its diet, the mandibles biting off pieces located by the upper and lower lips and the palps. We shall see

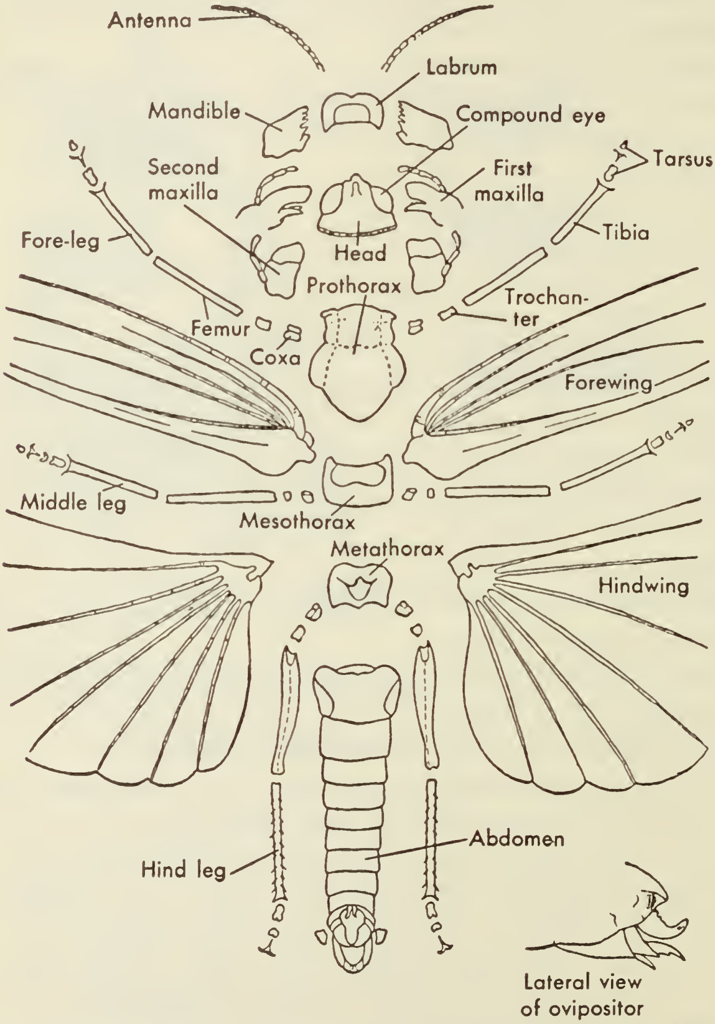

Fig. 23:16 External anatomy of a grasshopper (*Melanoplus*). Redrawn after Packard, *Textbook of Entomology*, The Macmillan Company.

later that in other types of insects these same mouth parts are adapted for sucking the juices of plants or the blood of other animals.

The **thorax** is divided externally into three segments or metameres named from anterior to posterior, **prothorax, mesothorax,** and **metathorax** (Fig. 23:14). Each of these bears a pair of legs, there being six in all, a number which is characteristic of insects and which has led to the use of the term "Hexapoda" for the group as a synonym for Insecta. Each leg is attached to the thorax by two short segments, the first being called the **coxa** and the second the **trochanter.** Next follow two long segments, the first called the **femur** and the second the **tibia** (Fig. 23:16). Lastly comes the **tarsus** consisting of three segments and ending in two **claws** with a pad between them called the **pulvillus.** Entomologists have found many points of resemblance between the bodies of insects and men and we have an example in the use of the terms "femur," "tibia," and "tarsus." In nearly all cases, however, these resemblances are purely superficial, since insects and men are built on fundamentally different plans. The **forewings** arise from the dorsal side of the mesothorax and the **hind wings** from the corresponding part of the metathorax. Numerous veins strengthen the thin membranous wings, which are not mere plates of chitin but contain living tissue.

The **abdomen** is without paired appendages except for the **ovipositors** which in the female surround the opening of the oviduct. When eggs are to be laid the ovipositors are thrust into the ground, making a cavity in which the eggs are deposited.

(2) INTERNAL STRUCTURE

The muscular system of most insects is exceedingly complicated, literally hundreds of muscles being involved in the movements of the body and its appendages. However, the principle upon which the muscles act can be well seen in the metathoracic or jumping leg of the grasshopper. The skeleton or rigid portion of the leg is external while the muscles and their attachments are internal. The insect jumps by suddenly straightening out its hind legs. In this an important part of the movement occurs at the joint between the femur and the tibia. This is a hinge joint and the axis of the hinge passes horizontally through

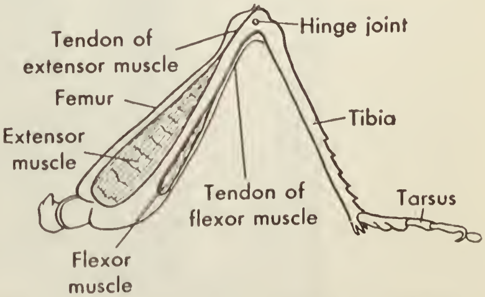

Fig. 23:17 Diagram illustrating the mechanism of leg movement in a grasshopper.

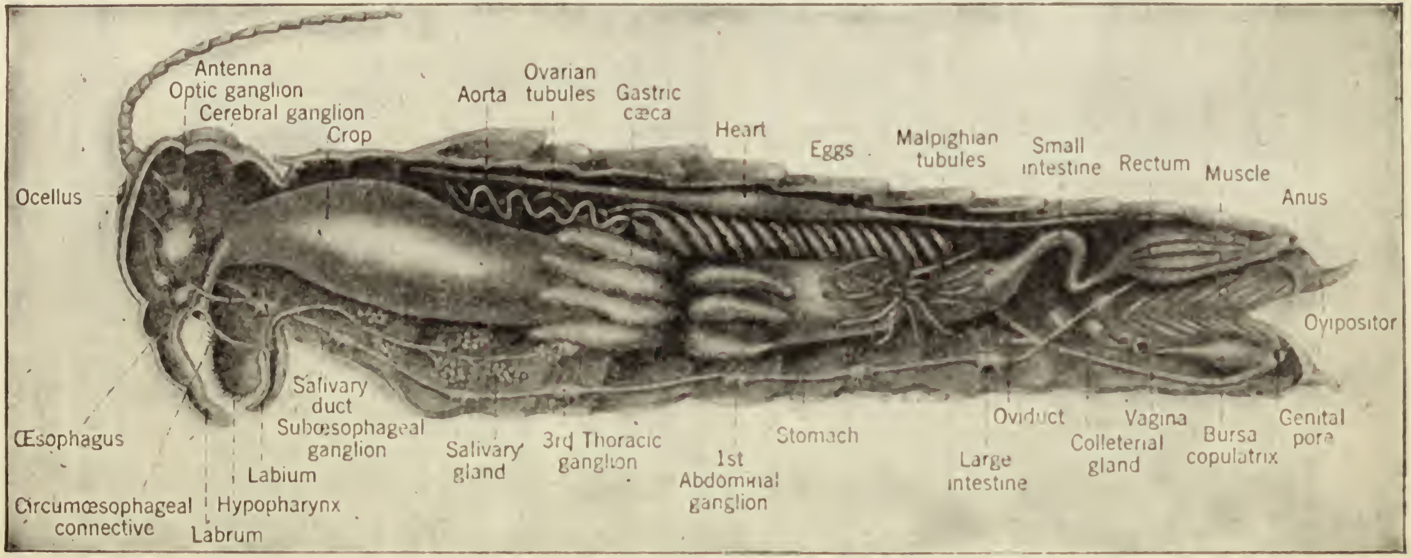

Fig. 23:18 Grasshopper. A lateral dissection showing the internal organs. The supraesophageal ganglion is here labeled cerebral ganglion. From Hegner, *College Zoology*, The Macmillan Company.

the center of the joint (Fig. 23:17). Two muscles move the tibia. One, called the **extensor,** extends it into line with the femur; the other, called the **flexor,** bends it in under the femur. These muscles are contained in the femur and are attached to it, the attachments being called the **origins.** The extensor muscle is much the larger and its attachment to the femur gives rise to a series of transverse ridges visible externally. The muscles end in long, thin tendons which are attached to the tibia. The tendon of the extensor muscle is attached to the portion of the tibia which is prolonged above the axis of the hinge, while the tendon of the flexor muscle is attached to the tibia below the hinge. In jumping, the extensor muscles are contracted, straightening the legs. If man were as good a jumper for his size as the grasshopper the record for the long jump would be somewhat over 100 yards.

Like the earthworm, the body of the grasshopper is built on the tube-within-a-tube plan, the exoskeleton and its attached muscles forming the outer tube, the digestive tract the inner tube (Fig. 23:18). The much reduced cavity between the two tubes is not a true coelom but a blood sinus or **hemocoel.** The true coelom is represented only by the cavities of the gonads.

The **mouth** is on the ventral side of the head. It opens into a small **oral cavity** which receives the ducts of a pair of **salivary glands.** The **esophagus,** which begins as a short tube, runs dorsally and then posteriorly to be enlarged in the thorax to form the **crop.** The crop is continuous with the **gizzard** or **proventriculus** which strains and crushes the food. Posterior to this is the **stomach** or **ventriculus,** also referred to as mid-gut. Into the anterior end of the ventriculus open six fingerlike diverticulae called **gastric caeca.** The posterior end of the ventriculus is continuous with the **intestine,** the region of transition being marked by the entrance of numerous fine tubes called **Malpighian tubules** which are excretory in function. The intestine consists of a large intestine, small intestine, and **rectum.** The **rectum** opens to the exterior by the **anus.** The whole of the digestive tube with the exception of the ventriculus is lined with chitin. Absorption takes place only through the walls of the ventriculus.

The **respiratory system** consists of numerous air tubes or **tracheae** leading into and out of **air sacs.** The tracheae divide repeatedly, sending branches to all the organs of the body and forming finer and finer branches, the finest of which are believed to enter the individual cells. Small openings or **spiracles** on the sides of the body, easily seen in the abdomen and thorax, place the tracheal system in communication with the outside air. The tracheal tubes are lined with chitin. If a grasshopper is watched when at rest or while held between the fingers, its abdomen will be noticed to expand and contract rhythmically. By these **respiratory** movements the air in the tracheal tubes is exchanged for fresh air from the outside. The respiratory system of insects is very different from that of the earthworm. In the latter animal oxygen coming in through the skin is transported by the blood to the cells of the tissues; in insects air is transported in the tracheal tubes directly to the cells.

Excretion is carried out by the **Malpighian tubules.** It is uncertain whether these tubules correspond morphologically to the nephridia of the earthworm which they resemble in function.

The **circulatory system** of insects is simpler than that of the earthworm and of most other arthropods. This is probably because of the highly developed tracheal system which renders such a system unnecessary so far as respiration is concerned. The so-called **heart** consists of a tube passing from posterior to anterior just under the body wall and dorsal to the digestive tube. From this vessel the blood passes out into spaces and returns to the pericardial cavity surrounding the heart.

The **sense organs** are well developed. Fine hairs on various parts of the body, especially numerous on the antennae, give the sense of touch. Small pits act as organs of smell and taste, those on the antennae being regarded as organs of smell, those near the mouth as organs of taste. The **compound eyes** resemble those of the crayfish, to the description of which the student is referred. In addition the head bears three smaller eyes with single lenses called **ocelli.** All are familiar with the sounds made by grasshoppers. The noise when they are at rest is made by drawing the femurs of the large hind legs across a particular vein of the hind wing. The sharper noise made when flying is produced by rubbing the fore and hind wings together. To hear these sounds, which are undoubtedly signals, the grasshopper has well-developed organs of hearing, located one on either side of the first abdominal metamere. Externally the organ consists of a tightly stretched drum, internally of an arrangement of sense cells and nerves.

The **nervous system** (Fig. 23:19) consists of a **supraesophageal ganglion** (sometimes referred to as the brain but not comparable to the brain of higher animals) connected by a pair of **circumesophageal connectives** to a chain of ganglia which extends along the ventral side of the body from anterior to posterior, the first being called the **subesophageal ganglion.** The supraesophageal ganglion sends nerves to the separate elements or ommatidia of the compound eye, to the ocelli, to the antennae, and to the labrum. The ganglia of the ventral chain do not show the primitive paired condition seen in the earthworm and the embryo of the grasshopper, but appear as single unpaired ganglia. The subesophageal ganglion is located in the head and sends nerves to the mandible, the first maxilla, and labium. It will be remembered that in the formation of the head six metameres are fused. In the embryo the ganglia of the first three metameres fuse to form the supraesophageal ganglion and those of the last three to form the subesophageal ganglion. The thoracic ganglia send nerves to the corresponding legs and to the wings. There are six abdominal ganglia. The fact that this number is less than the number of abdominal metameres is explained by the fusion of the first abdominal ganglion with the last thoracic and fusions within the abdomen.

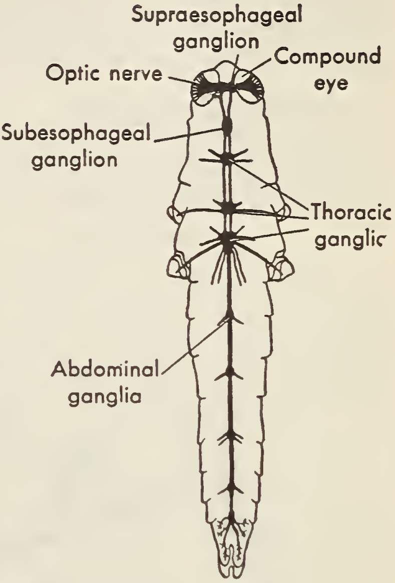

Fig. 23:19 The nervous system of a grasshopper (*Melanoplus*), dorsal view. Redrawn after Packard, *Textbook of Entomology*, The Macmillan Company.

The sexes are separate. The **testis** lies dorsal to the intestine and consists of two lateral halves united to form a single mass. From either side of this mass arises a **vas deferens,** which passes ventral to the intestine and after forming numerous coils unites with its partner of the opposite side in a single duct which passes into the copulatory organ or **penis.** This latter organ consists of four chitinous bristles which are used in transferring sperm to the seminal receptacle of the female. The **ovaries** are paired organs and lie in a position corresponding to that of the testis. Each consists of groups of **ovarian tubes** which open into the upper portion of the **oviduct.** The oviducts unite to form a short, straight **vagina** which opens between the ovipositors. Before its opening the vagina connects with the opening of the **seminal receptacle** which receives the sperm from the male at the time of copulation. The eggs are fertilized while they are in the vagina, just previous to being laid. The eggs are laid in the ground, the ovipositors being used to penetrate below the surface of the soil. The young which hatch from the eggs are called **nymphs.** They resemble adults, but are without wings and have somewhat larger heads in proportion to their size (Fig. 23:13).

C. THE HONEYBEE, *APIS MELLIFICA*

From the earliest times men have been interested in bees because of the honey which they produce and because of the organization and industry shown in their social life. A bee colony contains three kinds of individuals, the queen, the drones, and the workers. The present description applies to the worker, which is an immature female.

(1) EXTERNAL FEATURES

The body of the bee is sharply divided into head, thorax, and abdomen — a feature which is easier to see when the animal has been deprived of its numerous hairs (Fig. 23:20). The primitive metamerism of the body is much modified and it is only in the abdomen where the skeletal plates are arranged in rings that it is evident. In the abdomen each of these rings consists of a dorsal plate or **tergum** and a ventral plate or **sternum.** Terga and sterna are also present in the thorax and in addition lateral plates, called **pleura,** are interposed on either side between them. Six metameres are visible in the abdomen, but there are three more enclosed within the last visible metamere. What is in reality the first abdominal segment has moved up into the thorax and formed a part of it. There are no external evidences of metamerism in the head, but its embryological history shows that it is formed from six metameres.

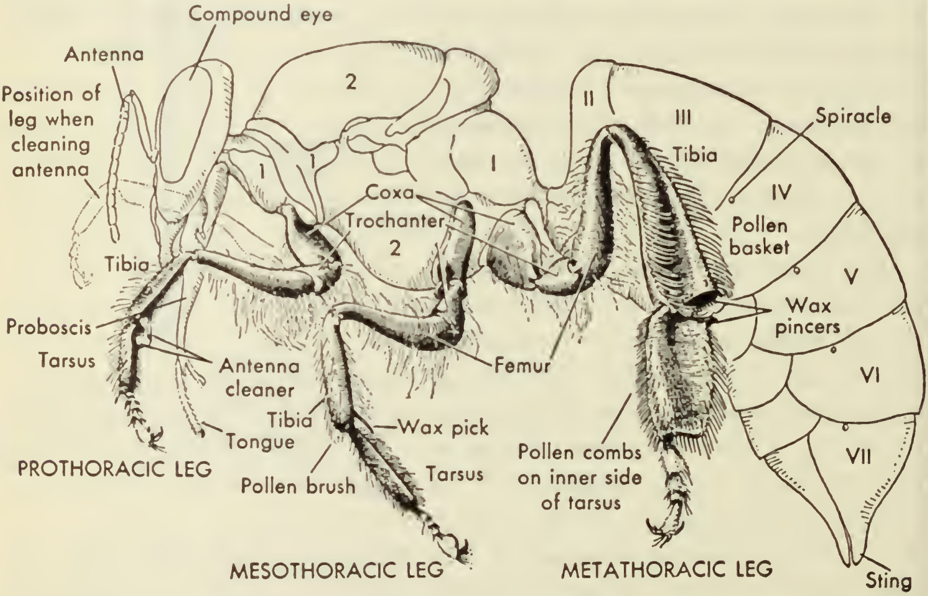

Fig. 23:20 The legs of the honey bee. For "wax pincers" read "pollen compressor." From L. L. Woodruff, *Animal Biology*, The Macmillan Company.

The head bears a pair of large **compound eyes,** one on either side set in flush with the surface, and on top at the corners of a triangle three small simple eyes, or **ocelli.** From the middle of the anterior surface a pair of jointed **antennae** project. The lower part of the head is occupied by the mouth parts. The upper lip or **labrum** is a flat plate attached to the front of the head. Behind this are the **mandibles** or jaws which are employed by the worker bee to knead the wax used in making the honeycomb. The next two pairs of parts, which are in reality appendages, are called the first **maxillae** (or simply maxillae) and the **labium** (or second maxillae). In the bee these parts are modified to form a long **proboscis** through which projects a still longer tongue or **hypopharynx.** The proboscis and tongue are used to suck nectar from flowers.

The three metameres of the thorax are named from anterior to posterior, **prothorax, mesothorax,** and **metathorax;** each bears a pair of walking legs. Everyone has seen the "busy bee" returning home burdened with yellow pollen. The walking legs are specially modified for the collection of pollen from flowers and its transport to the hive. A typical insect **leg** such as that of a grasshopper (Fig. 23:16) consists of a number of segments separated by joints. Nearest to the body come two short segments, the **coxa** and **trochanter;** next two long segments, **femur** and **tibia;** and lastly the **tarsus,** which consists usually of five small segments, the last ending in a pad with claws on either side. The modifications in the bee concern chiefly the tibia and the first segment of the tarsus, although all of the segments have long hairs and help in the collection of pollen (Fig. 23:20). The tibia of the first and second legs bear rows of hairs which form **pollen brushes.** In the first leg a spine from the end of the tibia fits over a semicircular notch in the side of the first segment of the tarsus forming an **antenna cleaner.** The antennae are cleaned by being pulled through the notch. A row of hairs on the opposite side of the segment forms an **eye brush.** In the second leg a spur from the tibia, called the **wax pick,** is used to remove the wax plates from the abdomen. In the third leg the first segment of the tarsus is broad and flat and the hairs are arranged in rows forming a **pollen comb.** The outer surface of the tibia is concave and surrounded by curved hairs forming a **pollen basket.** The pollen is packed into the basket by the pollen comb of the opposite leg for transport to the hive. At the joint between the tibia and the tarsus the ends of the segments are flattened, forming a **pollen compressor** formerly called the "wax pincers" but now known to be used to compress the pollen and pass it into the pollen basket.

The **forewings** are attached to the mesothorax and the **hind wings** to the metathorax. They join the body between the terga and the pleura.

TABLE 23:2. THE POLLEN-COLLECTING AND WAX-WORKING APPARATUS OF THE WORKER BEE

LEG	SEGMENT	FUNCTIONAL NAME
First	Tibia	Eye brush
	Tibia and first tarsal	Antenna cleaner
	First tarsal	Pollen brush
Second	Tibia	Wax pick
	First tarsal	Pollen brush
Third	Tibia	Pollen basket
	Tibia and first tarsal	Pollen compressor
	First tarsal	Pollen comb

The membranous wings are strengthened by veins which are thicker and stiffer in the neighborhood of the anterior margin and the articulation. On the anterior margin of the hind wings are hooks which catch on the forewings, making the two wings act together in flying. How the wings move to bring about flight will be discussed in a later section.

The **sting** is at the posterior end of the abdomen. The external parts consist of two palps or feelers which locate the place to be stung and a lancet which pierces the skin and through which the poison from a poison gland is injected. When a worker bee stings a person or other animal it usually leaves its sting and often also a portion of its abdomen in the skin. When more than the sting is left the bee dies, sacrificed for the protection of the colony. The parts of the sting of the bee are modified ovipositors and by some authorities are believed to represent abdominal appendages.

(2) INTERNAL STRUCTURE

The bee is a highly specialized insect both in its internal and external structure. It shows, nevertheless, the characteristic structure of an arthropod which includes the tube-within-a-tube type of body. As in most arthropods the coelom is greatly reduced. In the bee it is represented only by the cavities in the reproductive organs. The cavity surrounding the digestive tube and other organs is a blood cavity or **hemocoel** and not a true coelom.

The **body muscles** are attached to the exoskeleton and by their contraction cause movement at the joints. The muscular system of a bee is almost as complicated as that of a man. Some interest attaches to the muscles of flight and their action and they are therefore chosen for description and as an example of insect muscles. As already noticed, the anterior margin of the wing is rigid. When, therefore, the wing is moved up or down the posterior portion, which is flexible, lags behind. For this reason the upward and downward strokes of the wing are almost equally effective in thrusting the animal forward. The rapid vibratory movements of the wing are caused, chiefly, by what are called the **indirect wing muscles.**

These are large muscles which nearly fill the thorax (Fig. 23:21). Their action is indirect because they act not upon the wings directly but upon the tergum to which the wings are attached. The attachment of the wing to the tergum is such that when the tergum is pulled down the wing is raised. The muscles which bring this about extend from the tergum to the sternum. Their contraction flattens the thorax and raises the wings. The muscles which lower the wings extend from anterior to posterior. Their contraction shortens the thorax and at the same time raises the tergum. Other, much smaller muscles, called **direct wing muscles,** serve to move the wings in a horizontal direction, flexing them over the back or extending them for flight. A drone bee in flight has been shown experimentally to move its wings at the rate of 190 strokes per second.

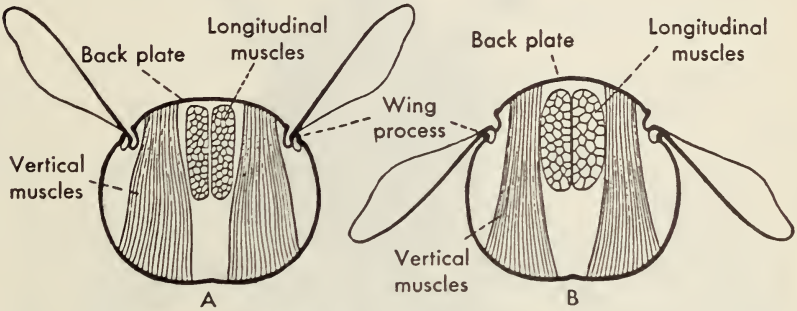

Fig. 23:21 The honey bee. Diagram to show movement of wings by indirect wing muscles. A, cross section of thorax through the wing processes with wings raised by the contraction of the vertical muscles which lower the back plate or tergum; B, the same, but with wings forced down by the contraction of the longitudinal muscles which raises the back plate or tergum. After Snodgrass, *Anatomy and Physiology of the Honeybee*, by permission of McGraw-Hill Book Company, Inc.

The diet of the adult worker bee consists of pollen and nectar. The nectar may be either taken directly or after it has been ripened into honey in the cells of the hive. Corresponding to this restricted diet is a specialized digestive system (Fig. 23:22). The **mouth** opens into a short pharynx which is followed by a thin, long **esophagus** extending through the thorax. In the abdomen the esophagus joins the **crop** or honey stomach, which when filled is a large balloon-shaped sac. At its posterior end the crop is continuous with a short section called the **proventriculus** which is partly evaginated into it, forming a valve which enables the bee to retain nectar or honey in its crop. All of the parts of the alimentary canal so far considered are formed from an inpocketing of the outer skin and are lined with chitin. The principal functions of the crop are to hold the nectar gathered from flowers during its transport to the hive and to carry honey.

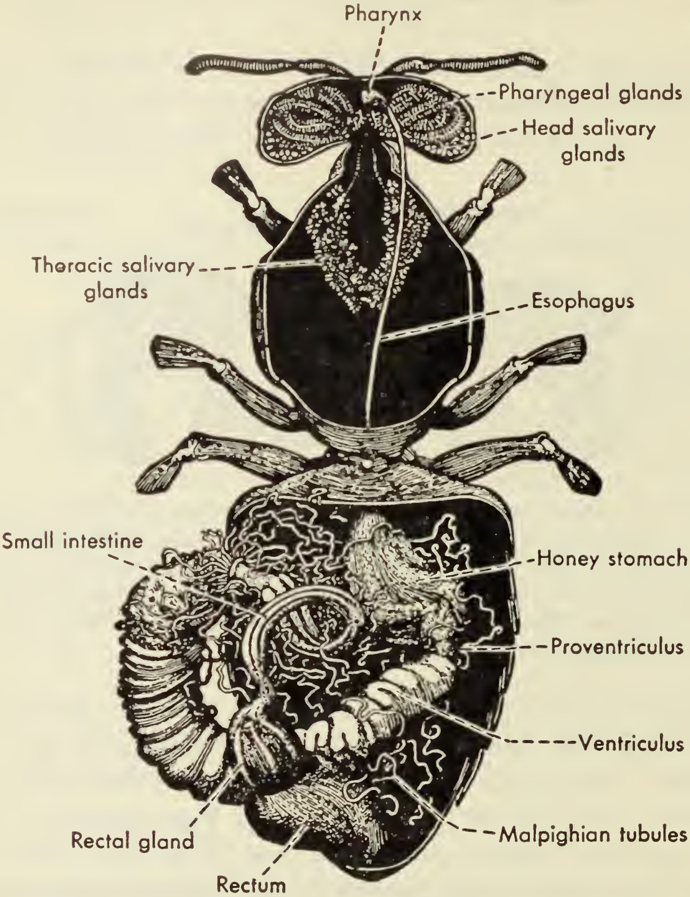

Fig. 23:22 The honey bee. Dissection of the digestive system of the worker bee, including associated glands. After Snodgrass, *Anatomy and Physiology of the Honeybee*, by permission of McGraw-Hill Book Company, Inc.

The only part of the digestive tract which is lined with endoderm and in which absorption can occur is that which follows the proventriculus and is called the **ventriculus.** This is also the largest part and is bent in the form of a U. The posterior end of the ventriculus is continuous with the **small intestine.** After making a single coil the small intestine leads into the **rectum,** an extremely distensible sac which opens to the exterior by the anus. The small intestine and rectum are formed by an inpocketing of the skin at the anus and are lined with chitin. Bees never defecate in the hive. During the winter so much fecal matter may be retained in the rectum that it may fill a large part of the abdomen.

Into the anterior end of the small intestine open numerous long, threadlike tubes called **Malpighian tubules.** These have been proved to be excretory organs.

Two pairs of **salivary glands** open on the anterior surface of the labium, i.e., into the mouth opening. The head glands secrete a fatty substance which it has been suggested may be used to soften the wax when it is kneaded. The secretion of the thoracic pair is used to dissolve solid food substances such as sugar.

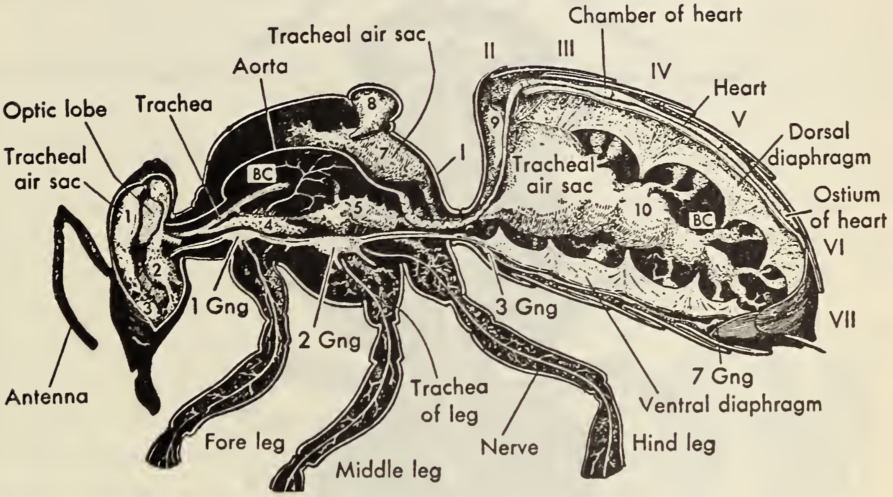

Fig. 23:23 The honey bee. Longitudinal section of the entire body of a worker bee, with muscles and digestive system removed, showing the air sacs and tracheae, the heart and aorta, and the nerve cord. 1–5, 7–10, air sacs; BC, body cavity (haemocoel); 1 Gng–7 Gng, ganglia of ventral nerve cord; I, II, III, IV, V, VI, VII, segments of abdomen. After Snodgrass, *Anatomy of the Honeybee*, by permission of McGraw-Hill Book Company, Inc.

The **respiratory system** (Fig. 23:23) consists of a series of **air sacs** and air tubes or **tracheae** which end in extremely fine tubules or **tracheoles** among the cells of the different tissues. The walls of the air sacs and tracheae are lined with chitin. Annular thickenings of the chitin prevent their collapse under pressure from the other organs. It is through the delicate walls of the tracheoles that the exchange of gases occurs. The tracheal system is placed in communication with the outside air through a series of openings called **spiracles,** visible on the abdominal segments. The air is changed in the air sacs by muscular movements of the body, easily seen when an insect is watched while at rest. The respiratory system of the bee and that of insects in general differs from that of an earthworm or a higher animal. In an earthworm oxygen is carried to and carbon dioxide away from the tissues in the blood. In an insect oxygen diffuses from the air sacs and tracheae through the tracheoles directly to the tissues and carbon dioxide diffuses directly outward along the same path.

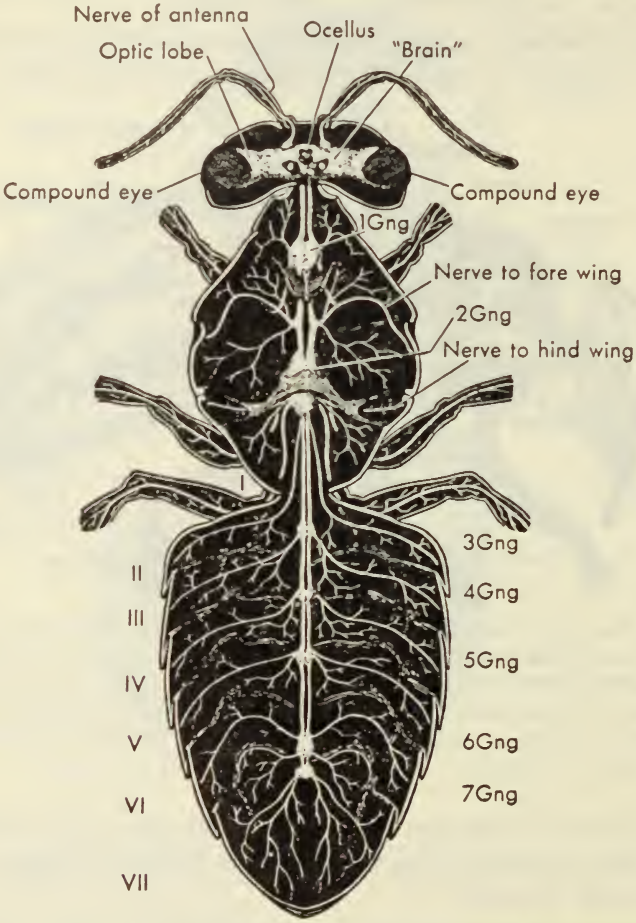

Fig. 23:24 The honey bee. The nervous system of the worker bee, dorsal view. The subesophageal ganglion is not shown, it is under the "brain." 1 Gng–7 Gng, ganglia of nerve cord; I–VII, segments of abdomen. After Snodgrass, *Anatomy of the Honeybee*, by permission of McGraw-Hill Book Company, Inc.

In consequence of the tracheal respiratory system and the lesser role played by the blood, the **vascular system** of the bee is relatively simple, consisting of a dorsal tubular heart which moves the blood through blood sinuses to the different parts of the body, there being no arteries or veins.

The bee is abundantly supplied with **sense organs.** On the antennae alone, seven kinds of different sensory organs have been described, not to mention the various kinds of sensory hairs found on the other parts of the body. Bees undoubtedly have a keen sense of touch and of smell, although there is some doubt as to whether they can taste. The **ocelli** can scarcely be called visual organs since they probably are able to distinguish only between different intensities of light and do not give an image. The **compound eyes** on the other hand are well-developed organs of sight. Their structure is similar to that of the crayfish eye. Certain organs in the legs suggest organs of hearing but there is some doubt as to whether they perform that function. Bees may be deaf.

The **nervous system** of the bee is highly organized (Fig. 23:24). The **supraesophageal ganglion,** sometimes referred to as the brain but really not comparable to the brain of vertebrates, is large. It consists of three pairs of ganglia fused into a single mass, and is continued on either side into large optic lobes connected with the compound eyes. The **subesophageal ganglion** which is formed from the fusion of the next three ganglia lies under the supraesophageal ganglion, separated from it by the pharynx and connected with it by short **circumesophageal connectives.** The ventral ganglionic chain consists of seven ganglia in addition to the subesophageal ganglion, two large ganglia in the thorax sending nerves to the wings and legs and five smaller ganglia in the abdomen. Into the formation of the second thoracic ganglion, which is much the largest, enter the ganglia from the second and third thoracic metameres and the first two abdominal metameres. The last abdominal ganglion is also compound, containing the ganglia of the seventh, eighth, ninth, and tenth segments.

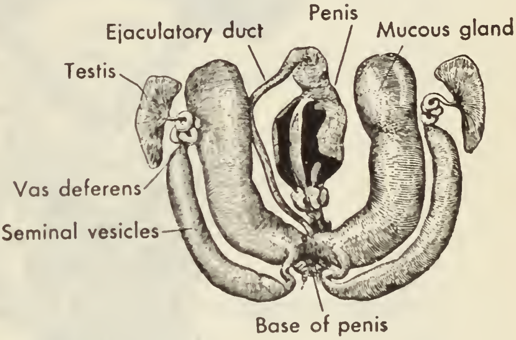

Fig. 23:25 The honey bee. Dorsal view of a dissection of the reproductive system of the drone bee (male). The opening through which the penis is everted is on the ventral side at the base and is not shown in the figure. After Snodgrass, *The Anatomy of the Honeybee*, by permission of McGraw-Hill Book Company, Inc.

The **reproductive organs** of the worker bee, which is an immature female, are rudimentary. In the queen and drone, on the other hand, these organs are large and highly developed. In the drone (Fig. 23:25) the paired **testes** connect with coiled **vasa deferentia** which lead into **seminal vesicles.** These latter connect with a single **ejaculatory duct** which passes to the **penis.** Connected with the ejaculatory duct are two large mucous glands. The penis is a rather complicated inpocketing of the outer skin into the abdomen, which is everted during copulation into the copulatory pouch of the female.

The **ovaries** of the queen bee (Fig. 23:26) consist of two large gourd-shaped masses which fill a large part of the abdominal cavity. These consist of numerous **ovarian tubules** which connect at their larger posterior ends with two short thick **oviducts.** The oviducts join to enter the vagina, a short wide tube leading to the **copulatory pouch,** a large inpocketing of the outer wall. Connected with the dorsal side of the vagina is a large sac, the **spermatheca,** in which the sperm received from the drone are stored. The eggs are formed in the ovarian tubules, the earliest stage occurring in the anterior ends and the more nearly mature eggs at the

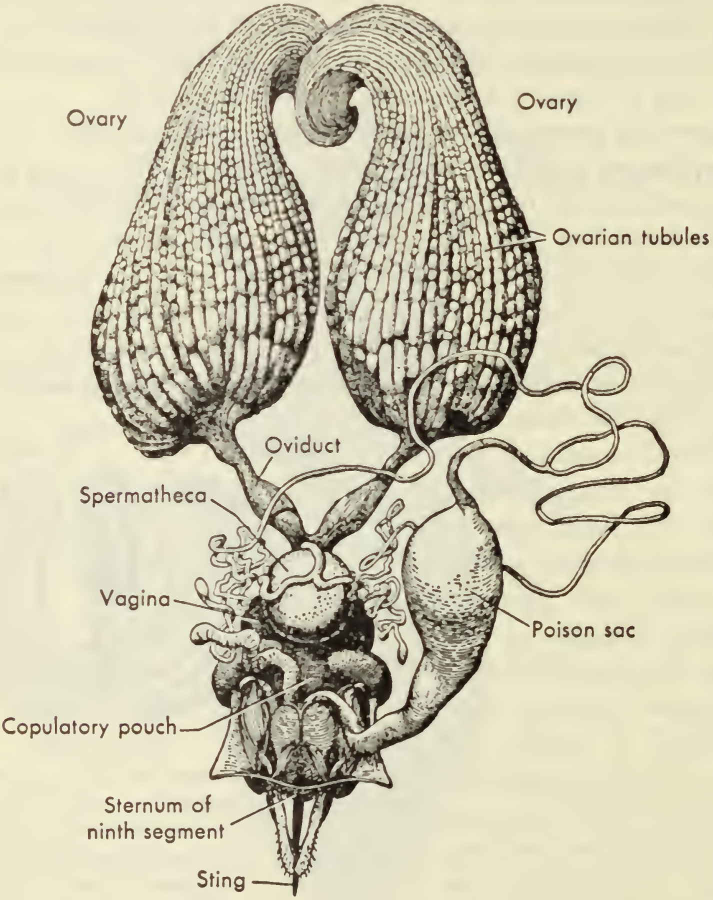

Fig. 23:26 The honey bee. Reproductive organs, sting and poison glands of the queen (mature female). The opening of the copulatory pouch is on the ventral side and is not shown in the figure. After Snodgrass, *The Anatomy of the Honeybee*, by permission of McGraw-Hill Book Company, Inc.

posterior ends where they connect with the oviducts. The eggs pass in single file down the oviducts and into the vagina.

A single queen bee may lay from one thousand to two thousand eggs per day. Normally as each egg passes through the vagina a few sperms are released from the spermatheca and fertilization occurs. The female has, however, the power of withholding the sperm from the egg and thus preventing fertilization. In the bee the fertilized eggs develop into female individuals (whether they become queens or workers depends on the diet they receive as larvae from the workers), while the unfertilized eggs develop into drones which are males. The development of an unfertilized egg is called **parthenogenesis**; it occurs not infrequently in certain groups of insects. The life history of the bee and the organization of the hive is discussed in the section on insect societies (Chap. 24).

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Questions

GENERAL QUESTIONS

1. What structural advances over the earthworm are shown by arthropods?
2. Name the three chief classes of the phylum Arthropoda and give their characteristics.

ON THE CRAYFISH

3. Describe a typical biramus appendage.
4. Taking the appendages in order from anterior to posterior show how each pair is modified from the typical biramus type to perform certain special functions.
5. Discuss whether the body plan of the crayfish is a tube-within-a-tube.
6. Explain the action of the muscles in closing the pincers.

7. Describe the digestive system of the crayfish.
8. Why is a current of water maintained through the gill chambers?
9. Describe the circulation of the blood.
10. Discuss the sense organs from the point of view of the sensations received by the crayfish.
11. Describe the nervous system. To what type does it conform?
12. Outline the life cycle of the crayfish.

ON THE GRASSHOPPER

13. Describe the mouth parts.
14. Describe the thorax and thoracic appendages.
15. Describe the action of the muscles which move the tibia.
16. Compare the digestive tract of the grasshopper with that of the earthworm.
17. Describe the respiratory system. Would such a system function under water?
18. Describe the circulatory system. Is it as highly developed as in the earthworm? Account for the difference.
19. Compare the nervous system with that of an earthworm.
20. Describe the male and female reproductive systems.

ON THE BEE

21. Compare the mouth parts of a bee with those of a grasshopper if you have studied that form.
22. Describe the thoracic appendages and show how each is adapted to perform certain functions in the food-getting of the bee.
23. Describe the action of the wing muscles in flight.
24. Show how the digestive tract of the bee is adapted to its diet and habits.
25. Describe the respiratory system.
26. Why is the vascular system relatively simple?
27. Describe the nervous system and compare it with that of an earthworm.
28. Describe the male and female reproductive organs. In what kinds of individuals do they occur?
29. Explain how the queen and the workers are able to determine what kinds of individuals are born into the colony.

Suggestion for Further Reading

Hegner, Robert W., *Invertebrate Zoology*, The Macmillan Company, New York, 1933, Chap. X.

CHAPTER 24

Arthropods (Continued). Metamorphosis, Serial Homology, the Arthropod "Mind," Insect Societies, Orders of Insects

1. METAMORPHOSIS

One of the most marvelous and at the same time most puzzling phenomena of nature is the change which many insects undergo in passing from the larval to the adult stage, called **metamorphosis,** from a Greek word meaning "to transform." In the simplest insects the young which hatch from the egg are like adults in all respects except size. In such insects there is **no metamorphosis**. There are only a few of these insects and they belong to the order Aptera. In many insects, for example the grasshopper, the transformation is gradual, occurring between molts. These insects are said to have an **incomplete metamorphosis**. The young, which in this case are called **nymphs**, resemble the adult in having the usual six legs and compound eyes; the wings, however, appear gradually, enlarging at each molt and do not reach their full size until the adult stage is reached.

Finally there are the insects like the butterfly in which the larva, called in this case a **caterpillar,** is very different from the adult. In the butterfly the caterpillar, after a more or less prolonged feeding period, spins a cocoon and goes into a quiescent **pupal stage** in which its anatomy is almost completely made over into that of the adult or **imago**. These insects are said to have a **complete metamorphosis**. The bee is such an insect, the larvae or grubs being raised by the workers in cells in the hive and undergoing their metamorphosis there. Such also are the many kinds of houseflies, the larvae or maggots living in decaying meat or other decaying matter, pupating there, and emerging as flies. Insects with a complete metamorphosis do not molt after emerging from the pupal stage and so do not grow in size after that time.

Insects are not the only animals which pass through a metamorphosis in their life history. Indeed, nearly all animals show changes in passing from youth to sexual maturity. In insects with a complete metamorphosis the change is very striking and is made more marked by the intervention of a quiescent pupal period. This divides the life history sharply into two stages: a larval stage which is given over to feeding, assimilation, and growth and an adult or imago stage which is given over to the propagation of the species and in which growth occurs only in exceptional cases.

Metamorphosis involves a breaking down of the cells and tissues of the larva and the building up of new cells and tissues from the products of the breakdown. These structural changes are accompanied by changes in the life and behavior of the animal. How different is the caterpillar, always intent on eating leaves, from the butterfly which flutters from flower to flower sucking nectar; or again the mayfly larva which crawls about under stones in streams eating voraciously for three years and undergoing an "incomplete metamorphosis" into the exquisite mayfly which lives for one night only, just long enough to mate and lay its eggs.

2. SERIAL HOMOLOGY

The repetition of the same plan of structure in successive pairs of appendages so evident in arthropods is an expression of the metamerism of the body. Since each metamere shows the same fundamental plan of structure it is not surprising that the appendages of successive metameres should also show a common plan of structure. While the term **metamerism** is used to describe the repetition of whole segments of the body, the term **serial homology** is used to describe the repetition of parts in successive metameres as seen in the appendages of the crayfish and to a lesser extent in those of the grasshopper and bee. Thus the different pairs of appendages of the crayfish are said to be serially homologous. **Serially homologous organs** may be defined as organs which are repeated in different metameres of the same animal and show in each metamere the same type of structure and the same relation to the other organs of the metamere and, as is seen in the mysis stage of the lobster, are also closely similar in their embryological origin and development.

The term **homology** is used for the same kind of relationship when it occurs, not in different metameres of the same animal, but in animals of different species. Thus in comparing a crayfish and a lobster the appendages of corresponding metameres would be homologous, i.e., the claw of the lobster would be homologous to the claw of the crayfish. **Homologous organs** may be defined as organs which, while occurring in animals of different species, show the same type of structure, the same relation to the other organs of the body, and a close similarity in their embryological origin and development.

It should be emphasized that **serial homology** and **homology** are morphological terms and have no reference to the function or functions of the organs; the serially homologous appendages of a crayfish or an insect may have entirely different functions. The modification of a part or the whole of an animal to perform a special function or to meet a special condition of the environment is called **adaptation.** Thus the antennules and antennae are adapted to act as organs of touch and taste, the mandibles for crushing food, the walking legs for walking, and so forth.

3. THE ARTHROPOD "MIND"

The student must be aware already of the essential similarity between the nervous systems of the Annelida and the Arthropoda. In both these groups the nervous system consists of a ventral ganglionic chain connected with a supraesophageal ganglion. Primitively the ganglia correspond to the metameres of the body, but in the arthropods there is a tendency toward fusion of the ganglia of contiguous metameres, especially in the anterior region.

In discussing the nervous system of the earthworm the path of a nervous reflex was traced. Similar reflex arcs occur in the arthropod nervous system and as in the earthworm the reflex may pass through one only or a number of ganglia. The study of the behavior of arthropods, and especially insects, seems to show that their various activities are best explained as due to reflexes. These reflexes may be interrelated, so that the reaction to a stimulus may act as a stimulus for a second reflex, and so on. Further the reflexes may be coordinated by nerve impulses passing from one ganglion to another in a different metamere.

The arthropod mind seems to be adapted to a stereotyped behavior. The solitary wasps provide interesting examples. Our most familiar wasps are the yellow jackets which make large paper nests in trees and under the eaves of houses. These are **social wasps.** The **solitary wasps,** although less likely to be noticed by the casual observer, are in reality the larger group. These wasps make their nests individually, either by cementing clay into tubes with a secretion from their salivary glands (mason wasps), by digging burrows or galleries in the ground (digger wasps), or by cutting tunnels in the wood of trees or the stems of plants (carpenter wasps). Those which make their nests in the ground are the most easily observed. The following account is based on the description in *Social Life among the Insects* by William M. Wheeler and refers to a solitary digger wasp of the genus *Sphex.*

After mating the female digs a slanting or perpendicular tunnel in sandy soil and enlarges its lower end to form a chamber. This completed, she closes the entrance to the tunnel and flies into the air, circling over the burrow in what is called a "flight of orientation" or "locality study" because it enables her to fix in her senses the exact position of the burrow in relation to the surroundings. Now she goes off in search of her prey which is a particular species of hairless caterpillar. When she finds one of these she stings it, chews its neck, and sucks some of its blood without, however, killing it. Then she drags it to the entrance to her burrow (Fig. 24:1). After opening up the entrance and a preliminary inspection she takes the caterpillar down into the chamber and fastens a single egg to the surface of its skin (Fig. 24:2), comes out and closes up the burrow which she leaves, never to return. As soon as the next egg matures she repeats the performance. The egg hatches into a larva which after eating the caterpillar spins a cocoon, pupates, and emerges as an adult wasp.

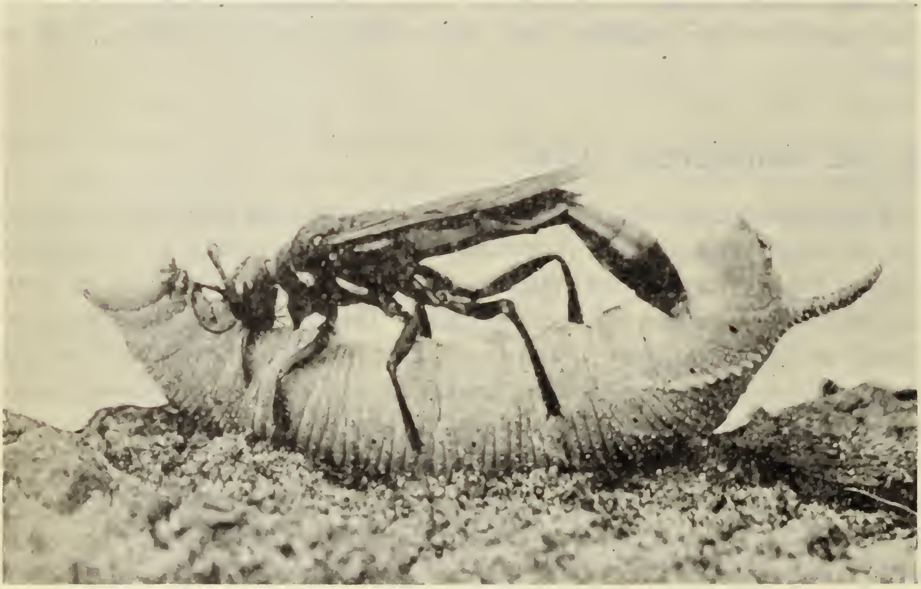

Fig. 24:1 A digger wasp (*Sphex procerus*) carrying a caterpillar of a sphinx moth to her burrow. Photograph by Professor Carl Hartman.

Since the mother does not rear her offspring and indeed probably never sees them there can be no question of their learning this rather complicated pattern of behavior. The most satisfactory explanation seems to be a series of reflexes following upon each other. Experiment has shown that the stinging of the prey follows as a reflex when the wasp seizes it and the underside of the wasp's body is touched by the caterpillar.

Not all solitary wasps use caterpillars to provision their nests. Some use beetles, others grasshoppers, others flies. One interesting group uses spiders: the giant tarantula killer provisions its nest with the giant tarantula. The social wasps provision their nests with the bodies of insects. A wasp colony consists of three kinds of individuals: males, a mature female (queen), and workers (smaller, sterile females). We will, however, pass to the bees and ants for a study of insect societies.

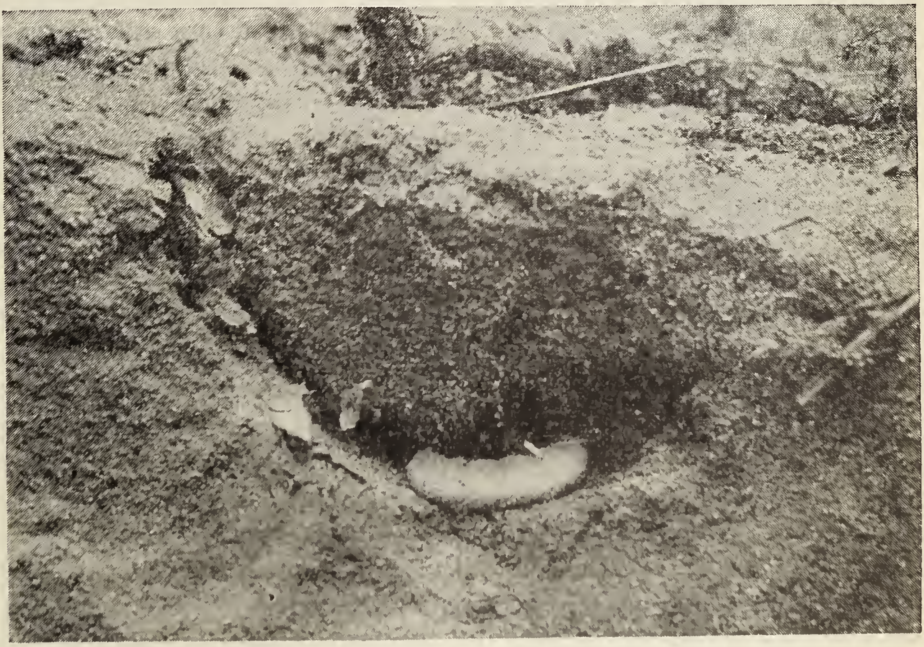

Fig. 24:2 The burrow of a digger wasp (*Sphex procerus*) in section showing filling of debris in the tunnel and the paralyzed sphinx moth caterpillar with the egg of the wasp glued to its side. Photograph by Professor Carl Hartman.

4. INSECT SOCIETIES

Insect societies have interested zoologists and social philosophers from the earliest times, on account of their striking peculiarities and their resemblances both real and fanciful to human institutions. Four different groups of insects have developed "social institutions," apparently independently of each other: the wasps, bees, ants, and white ants or termites, the last being quite different from the true ants in their structure and social organization. We will discuss the bees, ants, and termites.

Many bees, like wasps, are solitary diggers, carpenters, or masons. Their nests, however, unlike those of the wasps, are provisioned with vegetable food. A step toward a social organization is shown by certain species, which build their nests in groups connected by a common corridor with a single external opening. Our common bumblebees have a well-organized, although transitory, social system. The following description is based on that in Vernon L. Kellogg's *American Insects.* Three kinds of individuals occur, males or drones, fertile females or queens, and infertile females or workers. The workers are always smaller than the queens. Only fertilized queens live through the winter, hibernating in holes in the ground or hollow trees. When spring comes, each queen finds some deserted mouse's hole, mole's burrow, or other cavity in the ground and begins the founding of a colony. She gathers some pollen and honey, brings it to the hole, and there makes it into a round "pasty mass." On this lump of food she deposits from six to twenty eggs and then brings more food and deposits more eggs. The larvae which hatch out from the eggs feed on the pollen and honey and when full grown spin a silken cocoon. The bees which emerge from these cocoons are all workers. They enlarge the nest and bring in food. The queen continues to lay eggs, and the larvae which develop, when ready to pupate, are put in wax cells by the workers. As the number of workers is increased, the nest grows in size and may become as big as a man's head. Such a nest is composed of irregular wax cells most of which contain larvae, some pollen, and a few honey. At the end of the summer males and fertile females appear. These leave the nest and mate. When cold weather comes the workers and males die, leaving the fertilized females to continue the species.

The **honeybee** shows us the highest state of social organization found among bees. The common hive bee, *Apis mellifica*, kept in this country is an importation from the Old World. The different domesticated races, German or black race, Italian or amber race, and the Carniolan or striped race are all varieties of the same species. As in the case of the bumblebees a colony consists of a single **queen** or fertile female, a number of **drones** or males, and numerous **workers** or infertile females.

Under domestication bee colonies are kept in hives. The ordinary hive is simply a tightly closed wooden box with a small opening for the bees to enter. This, as far as the bees are concerned, takes the place of a hollow in a tree trunk or a burrow in the ground. In this wooden box are fitted vertical frames of thin wood about 4 inches square and 1½ inches wide, which are usually supplied with an artificial foundation of wax on which the bees build the honeycomb, consisting of small, hexagonal, wax-walled cells.

A prosperous hive in summer may contain sixty thousand to eighty thousand bees. Of these one is a queen, several hundred are drones, and the rest are workers (Fig. 24:3). In the central part of the hive are the brood cells. Here is found the queen passing from cell to cell laying a single egg in each at the rate of about one per minute. The eggs hatch in 3 days into soft-bodied, white, legless larvae which lie helplessly in the cells and are fed "bee milk," a mixture of digested honey and pollen, by the nurse workers. As each larva reaches the end of its larval period the cell is covered with wax by the workers and the larva within spins a silken cocoon and slowly changes into a pupa. Metamorphosis now occurs; the entire animal is made over both internally and externally. At the end of from 10 days to 2 weeks a worker bee gnaws its way out of the cell. The cell from which it has emerged is cleaned out and used either to rear another larva or to store pollen.

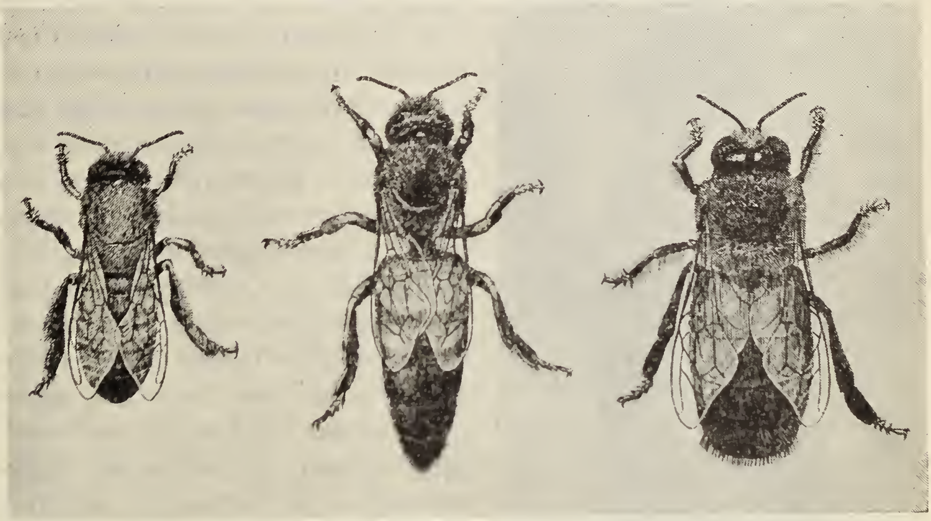

Fig. 24:3 The honey bee (*Apis mellifica*). Left to right, worker, queen and drone. Photographs by the U. S. Department of Agriculture, Bureau of Entomology and Plant Quarantine.

The majority of the cells, those not in the center of the hive, are used for storing honey. The worker bees collect nectar from flowers by sucking it into their crops or honey sacs. This they bring to the hives and regurgitate into the cells of the honeycomb. Here it is matured into honey by evaporation of a portion of the water which it contains and the addition of a small amount of formic acid, probably from the salivary glands of the workers, which acts as a preservative. The stored honey is used to feed larvae and to provision the hive during that part of the year when nectar and pollen are not available.

Certain of the brood cells are made slightly larger than the majority. Into these cells the queen lays eggs which will develop into male bees or drones. These larvae are fed by the workers in the same way as the worker larvae, but have rather longer larval and pupal periods.

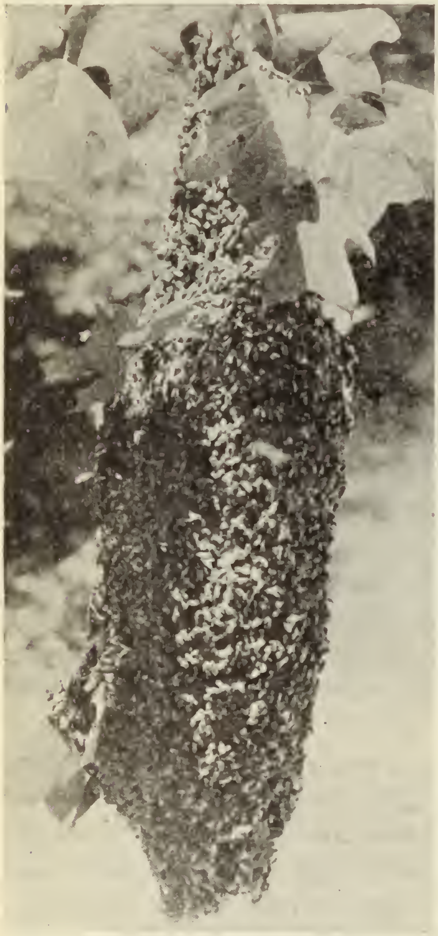

Fig. 24:4 A swarm of honey bees (*Apis mellifica*). Photograph by the U. S. Department of Agriculture, Bureau of Entomology and Plant Quarantine.

A bee colony grows rapidly during the early summer and when a colony shows signs of becoming too large for its hive, preparations are made for "swarming." Steps are taken by the workers to bring into the world a new queen. Some of the worker cells are greatly enlarged or new large cells are made. The larvae in these cells are fed for the first three days like worker larvae but after this they are fed lavishly on "royal jelly," a rich albuminous bee milk believed to be formed in the true stomach or ventriculus of the workers and regurgitated into the queen cells. The larval period of the queen larvae is approximately the same as that of the workers but the pupal period is shorter, about nine days.

Usually swarming occurs before the young queen or queens emerge, for the old queen cannot tolerate even her own daughters. The swarm consists of the old queen and a majority of the workers, only a few thousand being left to carry on the old colony. Before leaving the hive the bees fill their honey sacs with honey, enough to last them for several days. After leaving the hive, the swarm usually comes to rest on the branches of a near-by tree (Fig. 24:4). Sometimes some of the workers have previously selected a hollow in a tree or other suitable place for a new nest. In this case the swarm flies there en masse. Otherwise it waits restlessly while scouts are sent out in search of a new home. The beekeeper always tries "to hive" a swarm before it escapes to the woods. In their new nest the workers immediately begin to erect the honeycomb, and the queen to lay her eggs and found a new colony. The wax for the honeycomb is secreted by the workers from glands on the under side of the abdomen.

In the old colony when a new queen emerges there may be a second swarming or more usually the old colony may continue with the new queen. Now occurs the **nuptial flight.** A drone from the same hive will not mate with the new queen, at least in the hive. Choosing a bright sunny morning she flies out. From neighboring hives drones, which may be lazily sipping nectar, rise up and follow her. The queen flies higher and higher, outdistancing all but the more powerful males. Eventually one is successful, but in his success he dies, for copulation is fatal to the drone. The queen returns to the hive to continue the colony. A female copulates but once, the spermatozoa received into the spermatheca at that single copulation remaining alive during the whole of her fertile life, which is about three years.

The spermatheca opens into the vagina through which the eggs pass to be laid. The queen has the power to control the passage of sperms from the spermatheca and therefore to determine whether or not the egg will be fertilized. Females, workers and queens, are developed from fertilized eggs, males from unfertilized eggs. As already stated, whether a female develops into a worker or a queen depends on its food during the latter part of its larval life.

It is clear from this brief description of the bee colony that it is really a single family, the queen having given birth to the entire population which is, therefore, composed of brothers and sisters. Further, although the queen is carefully tended by the workers, she is not a ruler in the sense in which we use the word queen.

Ant nests are made in the open soil, under stones, or in rotten wood. The colony consists of a fertile female or queen, males, usually present only at certain periods, and workers which are infertile females. In many cases there are several different kinds or **castes** of workers adapted to special activities such as guarding the nest (soldiers), gathering food (workers proper), and nurse workers. These different castes are structurally different (Fig. 24:5) so that the species are markedly polymorphic. The driver and legionary ants are among the most conspicuous creatures of the tropics. They are the Huns and Tartars of the insect world, and move in vast armies which sometimes attack large animals and kill them. The harvesting ants collect seeds and store them in granaries underground. Some ants live in a close mutual relationship with plants. The fungus-growing ants make underground gardens in which they grow a particular species of fungus. Some species keep herds of aphids or plant lice which they pasture on the leaves of trees. From the aphids the ants obtain "honeydew," a sweet liquid which is really the excrement of the aphid. In the honey ants certain individuals transform themselves for the storage of the liquid, hanging from the roof of the nest where they are given plant juices or perhaps honeydew brought in by the workers until they swell into globular honey sacs. The workers of the slave-making ants go on expeditions to the nests of other ants, the workers of which they capture and bring to their own nests to work as slaves. Curiously enough the individuals of one of the commonest species of slave makers

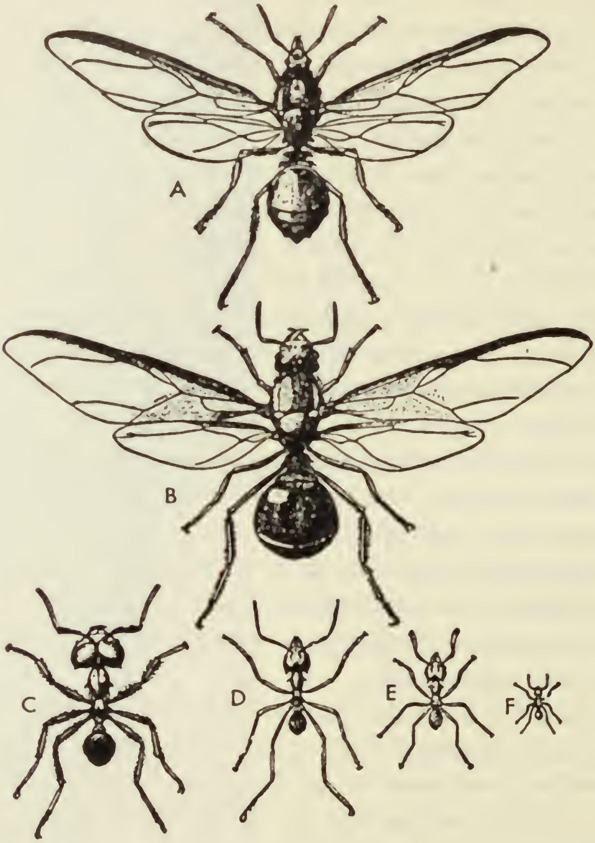

Fig. 24:5 Polymorphism in ants illustrated by the adult forms of *Atta* (*Oecodoma*) *cephalotes* taken from a single nest. A, male; B, winged female; C–F, various forms without wings; C, so-called soldier; D, large worker; E, smaller worker; F, smallest worker. All equally magnified. After the *Cambridge Natural History*, from Newman, *Outlines of General Zoology*, The Macmillan Company.

(Formica sanguinea) are of a ruddy color, while the slaves (Formica fasa) are black. The amazon ants have become so addicted to the practice of slave making that they have no true worker caste and are entirely dependent on their slaves.

The **termites,** called also white ants, are really not ants at all and belong to an entirely different order, the Isoptera. Although from many points of view they are primitive insects, having, for example, an incomplete metamorphosis, they have a complicated social system. They are all burrowing animals and are more abundant in warm countries where they are a serious pest, destroying buildings and furniture. "They have been known to enter a table through the bottom of the legs and to eat all the inner portions so that a slight weight crushed it to the floor." In Florida termites do much damage to orange and other valuable trees.

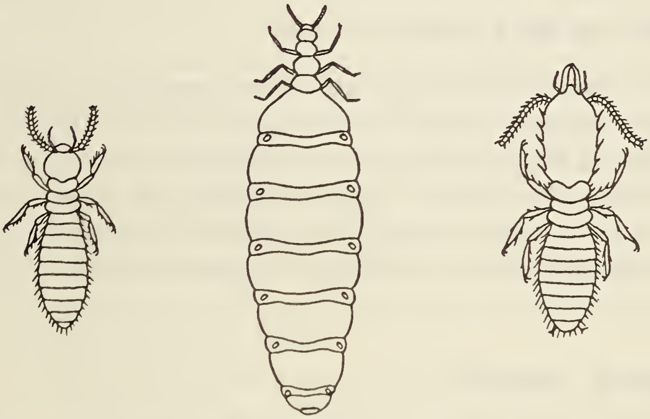

Fig. 24:6 *Termes flavipes*, a termite. On the left, a worker; in the center, a queen; on the right, a soldier. Redrawn from Comstock, *A Manual for the Study of Insects*, copyright by The Comstock Publishing Company, Inc.

A termite colony contains individuals of a number of different types or castes (Fig. 24:6). The worker castes, of which there may be several, varying in size and duties, consist of infertile males and females. There are also frequently soldier castes which likewise contain both sexes. These have relatively tremendous heads and jaws. The royal caste consists of kings and queens which, however, do not rule the colony and have little to say about its government. When full grown the kings and queens have wings. In May or June in the case of the common northern species they leave the nest and swarm. "After a flight of some distance the wings are shed, and a king chooses some queen near him and proposes that they start a kingdom of their own. But like mortal kings and queens they cannot reign unless a kingdom is found for them, and so millions of royal pairs die because they have no subjects. But sometimes a fortunate couple is discovered by some termite workers who at once take possession of the wanderers and provide them with food and with shelter in the shape of a large circular shallow cell."[1] The queen soon begins to develop eggs and her abdomen enlarges, forming a huge sac more like a potato than an insect, both in shape and in size. She is perfectly helpless and dependent on the workers who feed her and carry away the eggs which are laid in enormous numbers. The larvae which hatch from the eggs are fed by the workers.

5. INSECTS IN RELATION TO MAN

Insects are man's chief competitors in the struggle for existence. They eat his crops before he can harvest them and eat them after they are harvested, kill trees, lay waste forests, and destroy woodwork, eat his clothes, infest his body, and distribute horrible diseases. So important is man's war against insects that its study is the subject of a special science, applied entomology, and to it is devoted a special branch of the government.

A. USEFUL INSECTS

A few insects are exceptions to this general indictment and can be listed as producers of important economic products. Such are the bee and the silkworm. The honeybee is considered at length in this chapter. Honey is the nectar of flowers ripened in the cells of the beehive. Natural silk is obtained from the cocoons spun by silkworms or larvae of the silkworm moths, of which there are a number of species, the best known being *Bombyx mori* (Fig. 24:7). The larvae are fed on the leaves of the mulberry which is grown for the purpose. Silk culture requires a great deal

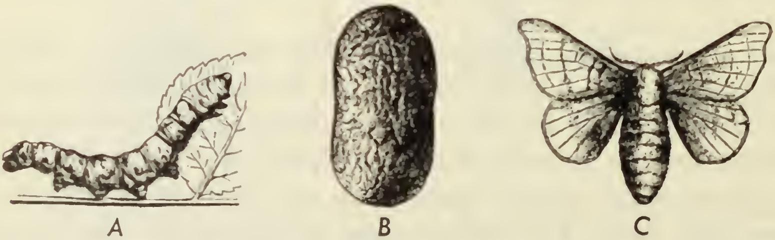

Fig. 24:7 Stages in the life-history of the silkworm (*Bombyx mori*). A, caterpillar; B, cocoon, from which the silk is obtained; C, adult female moth. After Shipley and MacBride, from Hegner, *College Zoology*, The Macmillan Company.

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[1] Quotations are from Comstock, *A Manual for the Study of Insects.*

of hand labor. China and Japan, where such labor is cheap, are the great silk-producing countries. Southern Europe was at one time an important source of natural silk, but the culture of silkworms is gradually being replaced by the more profitable manufacture of rayon and other silk substitutes.

B. INSECT PESTS

Mosquitoes have already been mentioned as the intermediate hosts of the parasites of three important diseases, malaria, yellow fever, and the disease caused by the filaria worm (filariasis). In each case a different species of mosquito is concerned. Malaria is transmitted by mosquitoes of the genus *Anopheles*, yellow fever by certain species of *Aedes* (*Stegomyia*), while the filaria worm is carried by mosquitoes of a number of different genera. There are also many other species of mosquitoes which suck the blood of man. Mosquitoes lay their eggs on the surface of the water in pools, bogs, reservoirs, and even tin cans. The larvae are aquatic and spend from one to three weeks in the water before going into the pupal stage. The pupae float at the surface of the water and give rise to the adult mosquitoes in from two to six days.

Various methods are used to combat mosquitoes but they all depend on doing away with the breeding places or destroying the larvae. Swamps and ponds are drained, cisterns screened. Where the water cannot be drained away it can be covered with a thin layer of kerosene or crude oil which prevents the larvae from breathing but this destroys the other animal life present. When it is impossible or undesirable to use either of these methods, natural enemies of the mosquito, such as minnows and dragonflies, may be introduced.

Houseflies are not only a pest to the housekeeper but they are a constant menace as the carriers of the germs of disease from person to person and place to place. The housefly is known to be a carrier of typhoid and is also believed to spread such diseases as tuberculosis, cholera, dysentery, smallpox, and diphtheria. The germs may be carried on the surface of the body of the fly, especially the feet and wings, or the fly may eat the germs with its food and pass them out in its feces. Experiments have shown that a single fly may carry over a million bacteria. The common housefly will breed in almost any kind of decaying organic matter but it seems to favor horse manure. Here the larvae feed, grow, and pupate. Flies and mosquitoes belong to the order Diptera.

Lice (Fig. 24:8) are small wingless insects which live on the skin of mammals and suck their blood. Three species infest man. The headlouse, *Pediculus humanus capitis*, lives in the hair of the head, where it lays its eggs and passes through its entire life cycle. The body louse, *Pediculus humanus corporis*, referred to as the clothes louse, or grayback, is the "cootie" of the First World War. It lays its eggs in clothing and to some extent lives there, obtaining its nourishment, however, by sucking blood. The body louse is dangerous as well as disagreeable since it transmits typhus fever, relapsing fever, and trench fever. The crab louse, *Phthirius pubis* (called also *Phthirius inguinalis*), lives on the skin and in the hair of the pubic and inguinal regions. The name refers to the fact that the legs stick out from the sides of its body like those of a crab.

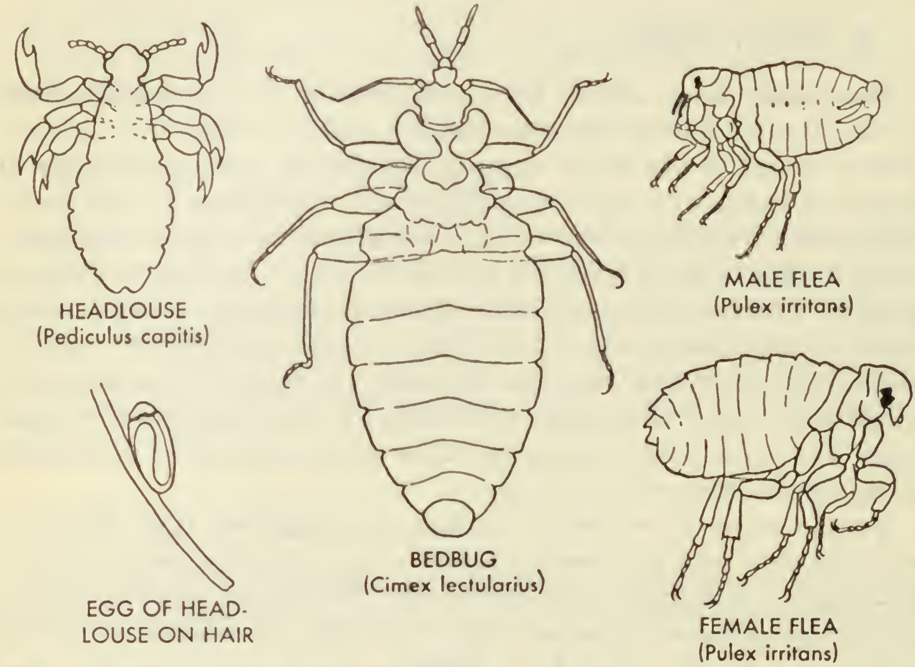

Fig. 24:8 External insect parasites of man.

The **bedbug,** *Cimex lectularius*, is a somewhat larger insect than the lice described above, with an oval abdomen, much compressed dorsoventrally, and either no wings or rudimentary wings (Fig. 24:8). During the day it hides in cracks or under carpets and at night goes abroad in search of its meal of blood.

The third group of insect parasites which plague mankind are the **fleas.** These small, laterally compressed, wingless animals are parasitic only in their adult stage when they live in the hair and suck the blood of birds and mammals (Fig. 24:8). Their larvae are wormlike and live in and on the dust and dirt which collects in cracks, under carpets, and in the folds of upholstery. The scientific name of the human flea is *Pulex irritans*. However, fleas are not very particular about their hosts and the fleas of domestic animals may annoy man. The Indian rat flea, *Xenopsylla cheopis*, is of importance as a transmitter of the bubonic plague.

C. INSECTS INJURIOUS TO CROP PLANTS

The **Hessian fly,** *Phytophaga destructor*, is the worst enemy of the wheat plant. This fly lays its eggs between the leaf bases and the stem. The larvae which hatch out eat their way into and through the stalk. Two or three broods are produced in a year. The larvae produced at the end of the summer remain in the pupal stage through the winter and hatch into flies in the spring.

The larvae of many species of Lepidoptera bore into the stems of crop plants and cause great loss to the farmer. Thus there is the European **corn borer,** *Pyrausta nubilalis*, which attacks other species of cultivated plants besides maize; the large cornstalk borer, *Diatraea zeacolella*, which attacks the young corn; and the sugar-cane borer, *Diatraea saccharalis*.

The **gypsy** and **brown-tail moths** destroy large numbers of trees in the New England states. The gypsy moth, *Porthetria dispar*, is an importation from Europe, having been brought to Massachusetts in 1866 by a well-meaning gentleman who thought it might be the means of starting a silk industry in that state. Some of the moths escaped and the insect became established in the vicinity, but was not recognized as a serious pest until some twenty years later. Since that time it has spread over most of New England. The eggs are laid in masses on the bark of trees, on walls, and in fact almost anywhere. The larvae eat the leaves of a number of different kinds of trees, including most of the common shade and fruit trees. The brown-tail moth, *Euproctis chrysorrhoea*, is another scourge of the forest introduced into Massachusetts from Europe. It was first recorded in 1897 and has since spread over New England and the adjacent Maritime Provinces of Canada. Like the gypsy moth the larvae feed on the leaves of fruit and shade trees. Gypsy and brown-tail moths cost the state of Massachusetts alone many millions of dollars each year.

The weevils (family Curculionidae) are a group of beetles. In the adult the head is prolonged into a long beak, sometimes as long as the body. The larvae are soft, wormlike grubs which feed on fruits and seeds. The cotton-boll weevil, *Anthonomus grandis*, was introduced from Central America and spread through Mexico to the cotton-growing states in 1890. It is now the cotton growers' most serious enemy. The beetles lay their eggs in the young bolls. The larvae which hatch out destroy the fruit. Different species of weevils attack the sweet potato, strawberry, plum, and many other fruits and garden vegetables.

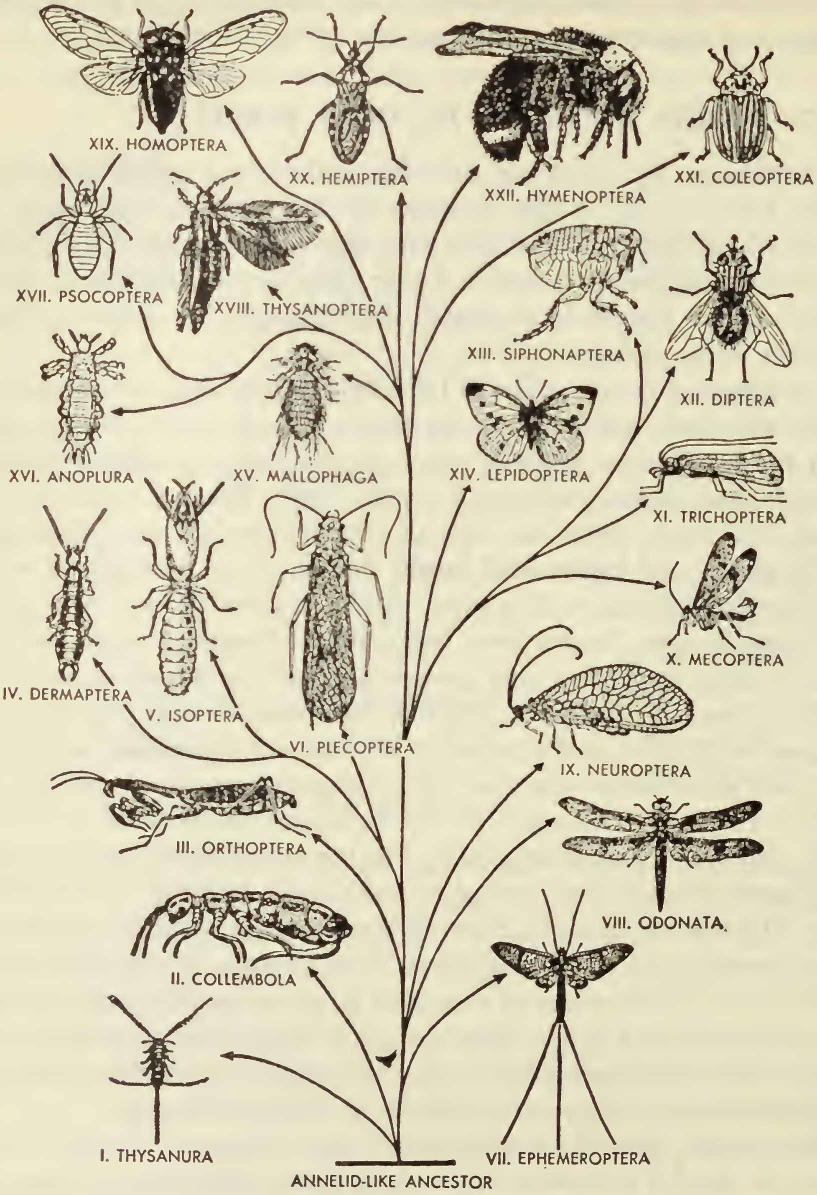

Fig. 24:9 Hypothetical phylogenetic tree of the class Insecta. I. Silverfish. II. Springtail. III. Praying mantis. IV. Earwig. V. Termite. VI. Stonefly. VII. Mayfly. VIII. Dragonfly. IX. Lacewing fly. X. Scorpion fly. XI. Caddis fly. XII. Stable fly. XIII. Flea. XIV. Butterfly. XV. Bird louse. XVI. Cootie. XVII. Book louse. XVIII. Thrips. XIX. Cicada. XX. Triatoma kissing bug. XXI. Potato beetle. XXII. Bumble bee. The figures are not drawn to scale. From Hegner, *College Zoology*, The Macmillan Company.

The insects which are most injurious to crops are nearly always insects which have been introduced from foreign countries. The reason for this is biological. In their natural habitats all insects have enemies which are often other insects which keep them in check. When they enter a new country or are artificially introduced their enemies are left behind. In many cases the introduction of these very enemies from the foreign countries has proved a successful method of control.

D. DESTRUCTIVE INSECTS

Many insects destroy the products of human industry. Two examples may be considered, the termites already referred to in the section on social insects, and the clothes moths. Termites attack particularly structures and articles made of wood. There are three species of **clothes moths,** the larvae of which live on woolen clothing and furs. The naked clothes moth, *Tineola biselliella*, is the most common. Its wings are of a light staw color. The case-bearing clothes moth, *Tinea pellionella*, is brown with three dark spots on each forewing. In the tube-building clothes moth, or tapestry moth, *Trichophaga tapetzella*, the forewings are black and white. In all three species the moths are small, having a wing spread of about $\frac{1}{2}$ inch. In each case it is the larva which does the damage.

6. THE INSECTS AS A GROUP

The class Insecta contains over 625,000 known species, more than there are known species of all other living things, plants, or animals, and no doubt there are hundreds of thousands of species not yet discovered. A brief classification showing the commoner orders of insects with examples is given in the Appendix. A complete classification is beyond the scope of this textbook. Works of many volumes have been written on single orders and even families. The evolution of the Insecta shows many divergent branches adapted and specialized for particular modes of life and particular environmental conditions (Fig. 24:9).

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1. Metamorphosis 473
2. Serial homology 474
3. The arthropod "mind" 475
4. Insect societies 477

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    A. Useful insects 484
    B. Insect pests 485
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    D. Destructive insects 489
6. The insects as a group 489

Questions

1. Name the different kinds of metamorphosis. Which kind would you expect to find in the most primitive insects?
2. Discuss the changes which occur at metamorphosis in a butterfly. What are the main biological differences between the imago and the larva?
3. Discuss the appendages of the crayfish, grasshopper, or bee with regard to their serial homology.
4. What is adaptation? Give examples from your study of the arthropods.
5. Give an example of instinctive behavior and discuss how it may be explained as a series of reflexes.
6. Compare a beehive or an ant nest with a human community.
7. Name nine orders of insects and give a brief account of each.
8. Place the following insects in the orders to which they belong: beetle, cockroach, "fish moth," butterfly, bee, grasshopper, housefly, wasp, dragonfly, aphid, white ant, caddis fly, moth, ant, cricket, cicad.

Suggestions for Further Reading

Wheeler, William M., *Social Life among the Insects*, Harcourt, Brace & Company, Inc., New York, 1923. Fascinating accounts of the social lives of insects by the greatest American authority on the subject.

Duncan, Carl Dudley, and Gayle Pickwell, *The World of Insects*, McGraw-Hill Book Company, Inc., New York, 1939.

Comstock, John Henry, and Anna Botsford Comstock, *A Manual for the Study of Insects*, Comstock Publishing Company, Ithaca, N. Y., 1895.

CHAPTER 25

Review of Phyla already Considered and Some Additional Phyla

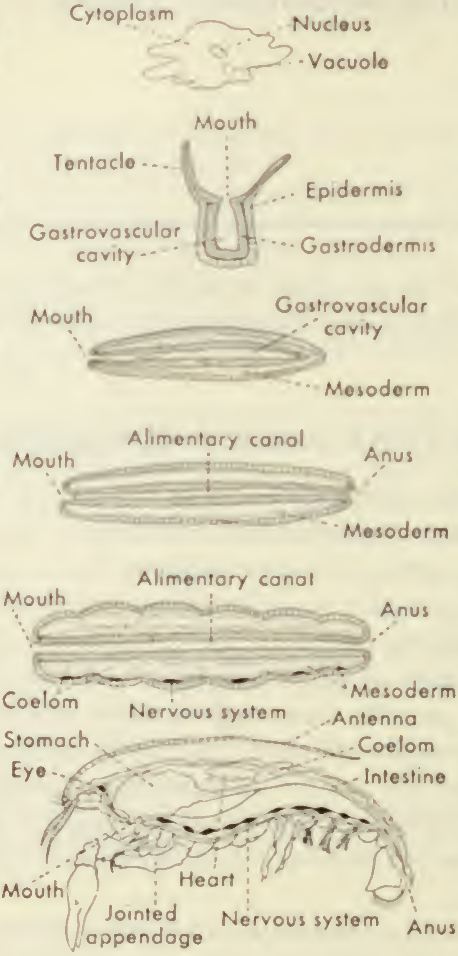
Before going further in the study of animal structure it will be well for us to review the progress of evolution in the types already considered (Fig. 25:1).

1. REVIEW OF THE PHYLA ALREADY CONSIDERED

PROTOZOA. Single-celled individuals or colonies of single-celled individuals. In many cases the individual cells show a high degree of differentiation but the progress of their evolution seems to be limited by the size which a cell many attain and the amount of specialization which can occur in the different parts of the protoplasm of a single cell. The formation of colonies of single cells may have been the method by which multicellular animals were evolved from simple, single-celled forms. The cellular structure of the more highly evolved protozoa, for example that of *Paramecium*, is quite different from the cellular structure of the cells of a multicellular animal such as *Hydra* or the earthworm. Animals like *Paramecium* are on a bypath off the general trend of evolution toward higher forms.

COELENTERATA. Saclike animals with a body consisting of two layers of cells, an epidermis or ectoderm and a gastrodermis or endoderm, surrounding a gastrovascular cavity. *Hydra* seems to represent a simple type of animal which may resemble the ancestor of higher types. The alternation of generations seen in this phylum is a special development and not related in any way to the development of higher forms as was found to be the case in the alternation of generations of plants.

PLATYHELMINTHES. The saclike structure of the coelenterates has been elaborated by the formation of a third kind of tissue, the mesoderm, and the development in it of special organs. Bilateral symmetry is associated with locomotion and a more active life than that of the coelenterates. The majority of the existing members of this phylum have taken to parasitism and manage to find a living under rather special conditions. These latter are to be regarded as having taken a bypath as far as the general course of evolution is concerned.



PHYLUM PROTOZOA	Single celled animals or colonies of single celled individuals
PHYLUM COELENTERATA	Sac-like animals with a body consisting of two layers of cells, ectoderm and endoderm, surrounding a coelenteron, or gastrovascular cavity
PHYLUM PLATYHELMINTHES	Sac-like triploblastic animals with bilateral symmetry
PHYLUM NEMATHELMINTHES	Bilaterally symmetrical, triploblastic animals with a tube-within-a-tube type of structure and a body cavity which is probably not a true coelom
PHYLUM ANNELIDA	Bilaterally symmetrical, triploblastic animals with a tube-within-a-tube type of structure, a true coelom, and metamerism
PHYLUM ARTHROPODA	Bilaterally symmetrical, triploblastic animals with a tube-within-a-tube type of structure, a true coelom (which is usually restricted), metamerism, jointed appendages, and well-developed cephalization

Fig. 25:1 The evolution of structure in six invertebrate phyla.

NEMATHELMINTHES. The tube-within-a-tube type of structure appears. The cavity between the two tubes is not, however, a true coelom and this fact raises considerable doubt as to whether these animals are on the line of descent of animals which, like the earthworm, have a true coelom. The phylum may be on a bypath.

ANNELIDA. Here the tube-within-a-tube type of structure is present with a true coelom and metamerism appears for the first time. There also appears a well-developed circulatory system and a nervous system of the ladder type. The annelid type of structure shows great possibilities and the phylum undoubtedly lies near to the main line of evolution of some of the higher forms.

ARTHROPODA. This phylum shows two advances: jointed appendages and cephalization. Although cephalization begins in the simpler phyla with bilateral symmetry and locomotion it is conspicuously developed here. Small but true coelomic cavities are present in the reproductive organs and at the internal ends of the excretory organs in the members of the phylum, and it seems possible that in the ancestors of this phylum there was a more extensive true coelom. The exoskeleton, although making possible the development of jointed appendages and a more active life, limits the growth and size of the animals and probably accounts for the relatively small size of arthropods in general as compared with vertebrates. One can scarcely say that the arthropods are on a bypath when the group includes at least half the known species of organisms. However, it is doubtful if the ancestors of any of the other phyla of the animal kingdom are to be found among them.

There are three important phyla not yet considered but which cannot be omitted in any survey of the invertebrates. They are the Porifera or sponges, the Echinodermata for which we have no inclusive common name, and the Mollusca or mollusks.

2. SPONGES (PHYLUM PORIFERA)

Sponges are widely distributed in both fresh and salt water. They vary considerably in size and shape. Some may reach a size of $2\frac{1}{2}$ to 3 feet in diameter. Others form thin colored incrustations on rocks. The presence of numerous pores on the external surface of the animal through which water is taken to the interior accounts for the scientific name of the group which means "pore bearers." The phylum Porifera does not seem to be on the main line of evolution of the more highly organized animals but possesses some biological interest on account of the abundance of individuals today and its long geological history. A convenient laboratory type is *Grantia* (Fig. 25:2), a little vase-shaped creature which lives permanently attached to rocks and wharf piles, just below low tide. The interior of the vase is occupied by a **gastral cavity,** and the opening at the

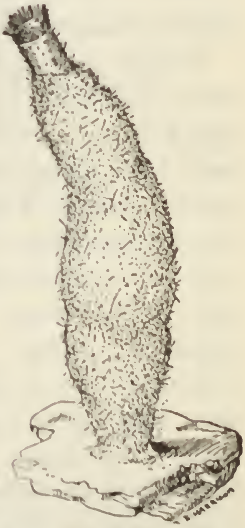


Fig. 25:2 *Grantia,* a simple sponge. From L. L. Woodruff, *Animal Biology,* The Macmillan Company.

top is called the **osculum.** Water enters the sponge through **pores** in the outer surface which communicate with the gastral cavity by canals (Fig. 25:3). In sponges of the type to which *Grantia* belongs, **incurrent canals** lead inward from the pores toward the gastral cavity but end before reaching it. Other canals, known as **excurrent** canals, extend from the gastral cavity toward the exterior between the incurrent canals but end before reaching the exterior. Connecting these two types of canals are shorter and smaller canals, called **prosopyles,** which connect the incurrent and excurrent canals.

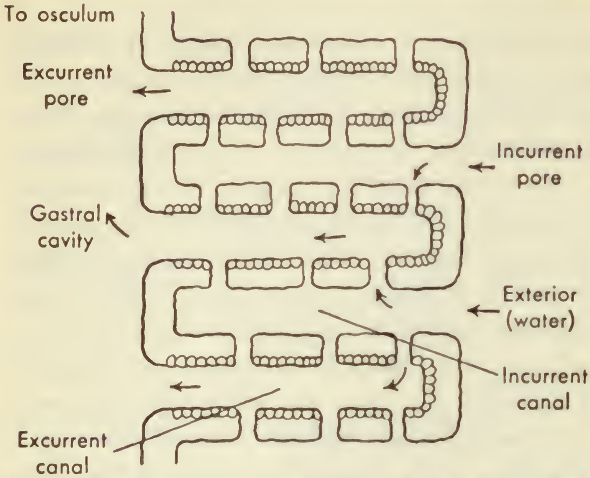


Fig. 25:3 Diagrammatic section of the wall of a sponge, showing canal systems. On the left is the gastral cavity of the sponge; on the right the exterior. Prosopyles connect the incurrent with the excurrent canals.

A layer of cells, called the **dermal epithelium,** which has been found not to correspond with the epidermis of *Hydra*, covers the outer surface of the sponge and lines the incurrent canals. The gastral cavity and the excurrent canals are lined with an epithelium which in the case of the latter canals is composed of peculiar cells resembling a certain type of flagellated protozoon, and called **collar cells** (Fig. 25:4). The inner epithelium has been found not to be comparable or homologous with the endoderm of *Hydra*. The collar cells create the currents by which water is caused to enter at the pores and pass through the incurrent canals, prosopyles, and excurrent canals to the gastral cavity and out through the osculum.

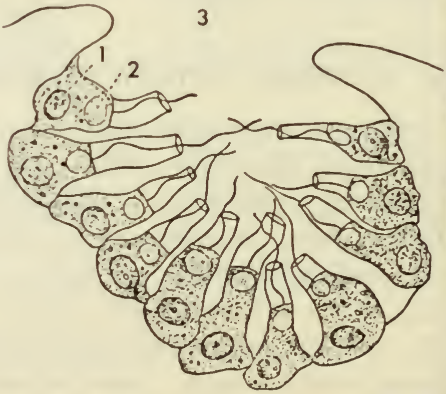


Fig. 25:4 Section of an excurrent canal of a sponge, highly magnified to show the collar cells and flagella. 1, nucleus of collar cell; 2, vacuole in collar cell; 3, excurrent canal. After Shipley and MacBride, from Newman, *Outlines of General Zoology*, The Macmillan Company.

Between the dermal and gastral epithelial layers is a gelatinous material containing amoeboid cells. The skeleton of *Grantia*, like that of most sponges, consists of minute **spicules** which are formed by cells in the dermal layer. Some spicules of a sponge are illustrated in Fig. 25:5. The spicules provide the sponge with rigidity. Sponges are classified mainly according to the composition and form of the spicules. In some sponges, as in *Grantia*, they are calcareous and composed of carbonate of lime; in others they are siliceous and composed of silicon, as in the beautiful Venus flower-basket. In other sponges fibers of a peculiar substance called **spongin** may be combined with siliceous spicules to make the skeleton. In others, as for example the bath sponge, the skeleton may consist of spongin fibers only.

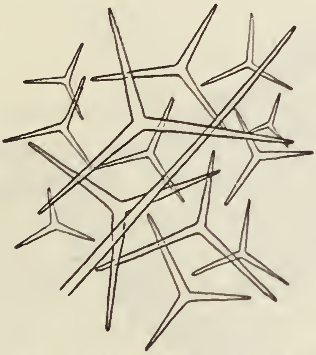


Fig. 25:5 Sponge spicules.

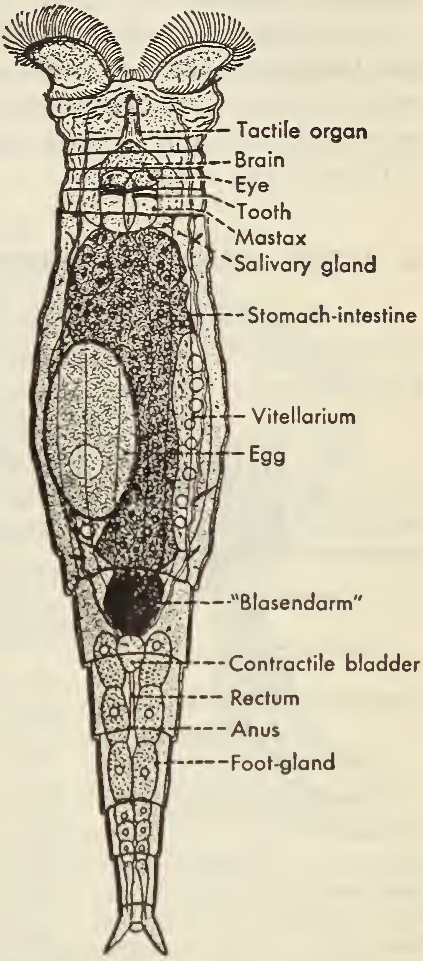


Fig. 25:6 A rotifer (Philodina), a common fresh-water species. A dorsal view of a living, extended individual. From Hegner, *College Zoology*, The Macmillan Company.

3. ROTIFERS (PHYLUM ROTIFERA)

A few drops of pond water when examined under the low power of the microscope will usually show numbers of rotifers (Fig. 25:6) which on account of their small size and ciliated movement may be confused with Protozoa. The cilia are usually arranged in two circles or wheels at the anterior end near the mouth. All confusion with Protozoa will be dispelled when the internal organs are studied. There is a digestive system consisting of a **mouth** and **pharynx** leading into a chewing stomach or

mastix which is provided with chitinous jaws that are constantly in motion. This is followed in turn by a larger **stomach-intestine** which is usually filled with food. A short rectum leads to a posterior **anus.** There is a pair of **excretory tubes.** The body cavity is not a true coelom. The sexes are separate.

An interesting feature is the production of **summer eggs** which develop **parthenogenetically,** i.e., without fertilization, and **winter eggs** which, when fertilized, develop into females. By secreting a gelatinous envelope some rotifers are able to resist drying up and live through great extremes of drought and temperature.

4. MOSS ANIMALS (PHYLUM BRYOZOA)

The Bryozoa (Fig. 25:7) are interesting chiefly on account of their abundance in the sea, especially in the shallow water near the seashore. Like the rotifers they are minute multicellular animals. In most species the individuals are associated to form colonies attached to rocks, seaweed, and so on. The resemblance to the mosses (Bryophyta) is rather fanciful. They are more apt to be confused with hydroids to which they bear a considerable superficial resemblance.

The individual consists of a body wall which in many forms secretes a hard outer covering forming a boxlike structure into which the soft parts may be retracted. The mouth is surrounded by ciliated tentacles somewhat like those of a hydroid and which, like them, carry food to the mouth. The digestive tract is U-shaped and consists of esophagus, stomach, and intestine which opens to the exterior by an anus. The Bryozoa are divided into two classes: class Entoprocta and class Ectoprocta. In the Entoprocta the anus opens to the exterior within the crown of tentacles. In the Ectoprocta it opens outside the crown. There is a true coelom in which the digestive tract is suspended in the Ectoprocta. A pair of nephridia are present in the Entoprocta. The individuals are hermaphrodites possessing both ovary and testis. From time to time the internal organs are discarded and a complete new set is formed from the body wall.

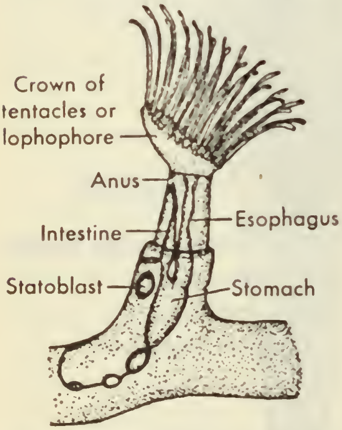


Fig. 25:7 A bryozoan. A diagram showing the structure of a single individual. From Hegner, *College Zoology*, The Macmillan Company.

5. THE LAMP SHELLS (PHYLUM BRACHIOPODA)

The Brachiopoda (Fig. 25:8) are of interest chiefly because of their long and abundant fossil history. Their bivalved shells resemble those of a mollusk. However, while the shell of a clam, for example, consists of right and left halves, hinged on the dorsal side of the animal, the shell of a brachiopod consists of dorsal and ventral halves hinged at the end. A pair of large ciliated **arms** occupies a large part of the space enclosed by the valves of the shell. These pass food to the mouth which leads into a stomach followed by an intestine. A true **coelom** is present and contains, in addition to the digestive organs, a pumping organ called the **heart** and a pair of **nephridia**. The sexes are usually separate.

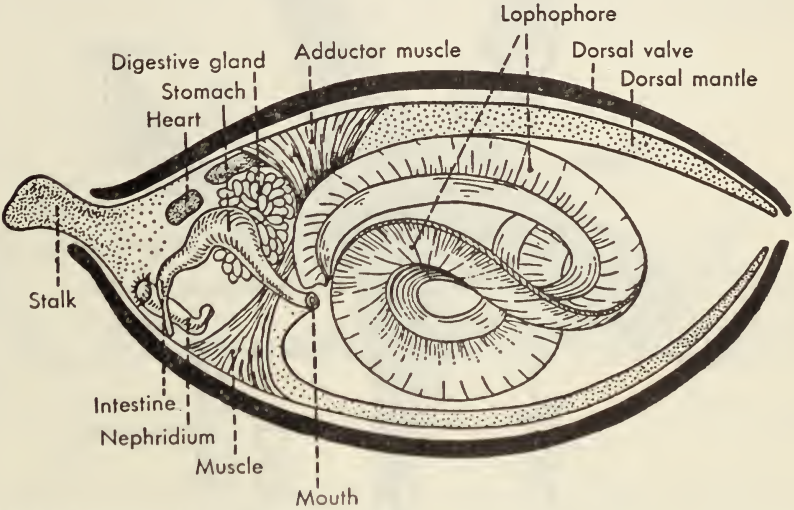


Fig. 25:8 Brachiopoda. Diagram of a sagittal section of an individual. The arms form the lophophore. From Hegner, *College Zoology*, The Macmillan Company.

6. ECHINODERMS (PHYLUM ECHINODERMATA)

The echinoderms are spiny-skinned marine animals. A familiar example is the starfish which will be described briefly.

The starfish (Fig. 25:9) is a radially symmetrical animal in which respect it resembles *Hydra*. From a central portion or **disc, arms** or **rays,** usually five in number, extend out like the points of a star. As the starfish is usually seen on a rock or on sand its mouth is at the center of the under surface which, because it contains the mouth, is called the **oral surface.** In this position the upper surface is called the **aboral surface.** At its center is the **anus.** The outer surface of the body is covered with **epidermis.** The hard skeleton, which is so conspicuous in a dried specimen, is an internal skeleton or endoskeleton consisting of numerous small **calcareous plates** or **ossicles.** The plates are arranged to form a more or less continuous but flexible skeleton which can be moved by bands of muscles extending between the ossicles. The spines which stick out all over the animal are endoskeletal structures and are covered with epidermis. Also projecting from the surface are numerous minute spines modified to form little pincers called **pedicellariae,** and small, soft, fingerlike processes which function as respiratory organs and are hence called **dermal branchiae.**

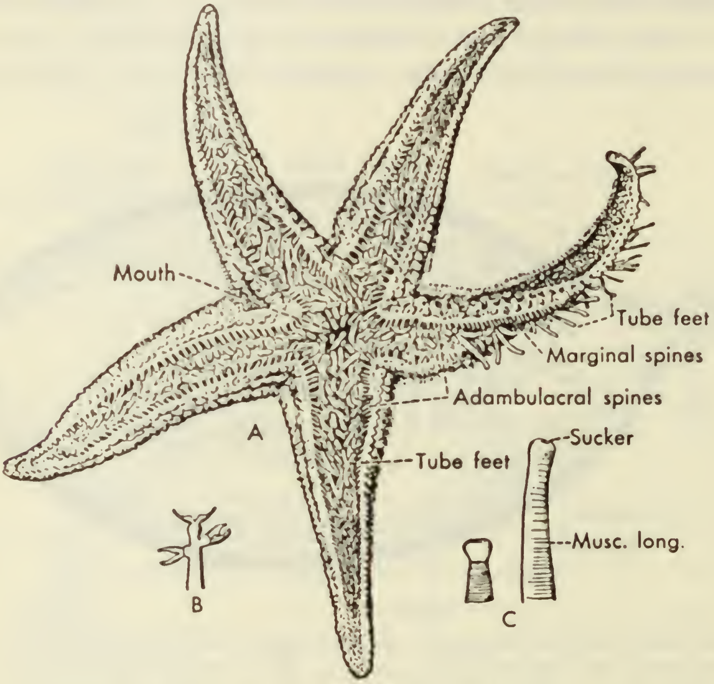


Fig. 25:9 A starfish, *Asterias rubens.* A, seen from the oral surface. The region around the mouth is depressed and the depression is continued into the arms as the ambulacral grooves. In these grooves and around the mouth are the tube feet protected by adambulacral spines extending from the margins of the grooves. B, a spine with pedicellariae; C, a tube foot contracted and expanded. After *Cambridge Natural History,* from Hegner, *College Zoology,* The Macmillan Company.

Along each arm the oral surface is folded inward to form an **ambulacral groove** which extends from the tip of the arm to the mouth. In these grooves are **tube feet,** small muscular tubes filled with water and ending in small vacuum discs called **suckers** which enable the starfish to catch hold of a rock or other object and either to move the object toward itself or to pull its own body toward the rock. The tube feet are connected with a complicated system of canals and vesicles, called the **water-vascular system,** which will not be described here.

The body wall including the endoskeleton surrounds a large body cavity which contains various internal organs and is a true **coelom** (Fig. 25:10). The mouth leads into a relatively large, thin-walled **stomach** from the upper or pyloric portion of which much-branched **pyloric caeca** extend into the arms. Starfish feed on shellfish, marine worms, and small crustacea. In eating a mussel or clam the starfish first opens the valves of the shellfish by catching hold of them with the tube feet of opposite arms. After this the stomach is partially turned inside out and envelops the soft parts of the clam or mussel while they are still in the shell. In this way the edible portions are gradually digested, passed from the stomach into the pyloric caeca, and absorbed. The respiratory organs, or dermal branchiae, were referred to previously in considering the external features. They consist of small saclike structures with cavities communicating with the coelom.

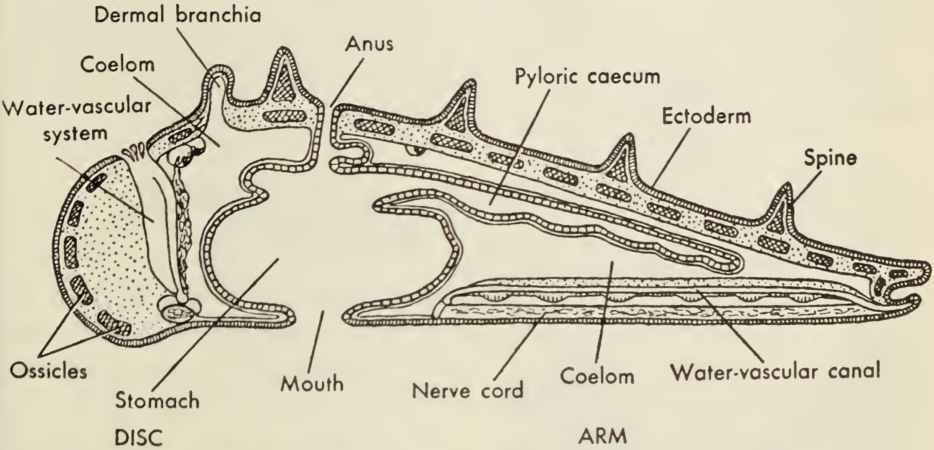


Fig. 25:10 A longitudinal section through the basal disc and one arm of a starfish. The epidermis is here labeled ectoderm.

The starfish is without special blood vascular or excretory systems. Absorbed food and waste materials are carried in the coelomic fluid. At the end of each arm is a simple eye consisting of cells containing pigment. The tube feet are also sense organs. The nervous system consists of nerve cells in the epidermis and some of the deeper tissues and of nerve cords extending to different parts of the body.

The sexes are separate and the **reproductive organs,** very much alike in the two sexes, are located at the bases of the arms. The eggs and sperm are extruded into the water where fertilization takes place. The early development of the starfish is described in Chap. 36. This development leads to the formation of a larva, which, unlike the adult, is bilaterally symmetrical.

Adult echinoderms are **radially symmetrical,** the principal organs being repeated and arranged like the spokes of a wheel about a central axis. They are triploblastic, have a well-developed coelom and usually an anus. Their skeleton is an endoskeleton composed of calcareous plates. Except in the attached forms, locomotion is by means of tube feet. They are all marine animals.

Echinoderms are of interest not only because of their abundance at the present time in the sea but also because of their long and extensive fossil record.

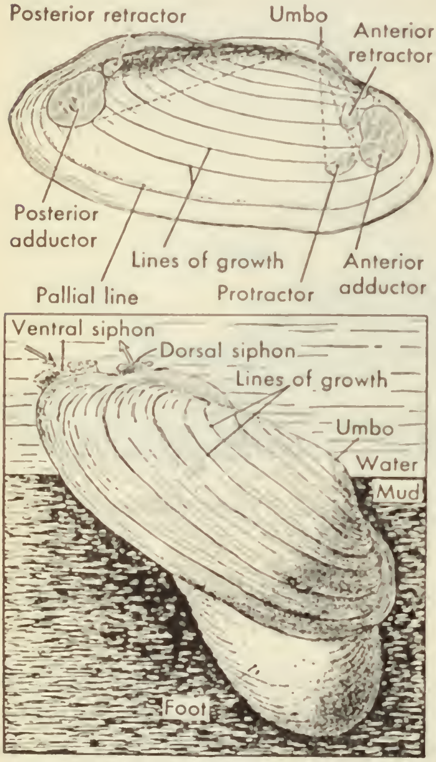


Fig. 25:11 A fresh water mussel. Above, interior of shell; below, view of the animal in its natural position in the mud at the bottom of a pond or stream. After Shipley and MacBride, from Hegner, *College Zoology*, The Macmillan Company.

7. MOLLUSKS (PHYLUM MOLLUSCA)

As an example of this phylum we may take a fresh-water mussel, *Anodonta*, of which there are numerous species.

The shell of this animal consists of two symmetrical halves or **valves,** hinged together by a tough elastic ligament (Fig. 25:11). The animal is bilaterally symmetrical and the hinge marks the dorsal side, the opposite side being ventral. The surface of each valve shows lines of growth which center about a small bulge at one end of the hinge called the **umbo.** When the mussel is in its natural habitat, in the mud or sand of ponds or streams, the valves are slightly separated and from the ventral side at one end, which is distinguished as anterior, there projects a fleshy mass called the **foot,** while from the other end project two short tubes of which the more dorsal is the **exhalent siphon** while the more ventral is the **inhalent siphon.**

When the valves are pried apart they are seen to be lined with a soft membrane called the **mantle** which is continuous with the tissue of the siphons (Fig. 25:12). The shell, which is mostly calcium carbonate, is secreted by cells in the mantle. The mantle surrounds a cavity, the **mantle cavity.** Into the central portion of this cavity the foot projects, and into the lateral portions the large platelike **gills,** a pair on each side. Two large adductor muscles, one anterior, the other posterior, extend between the valves of the shell. The contraction of these muscles closes the shell. The inner surface of the mantle and the surfaces of the gills are ciliated.

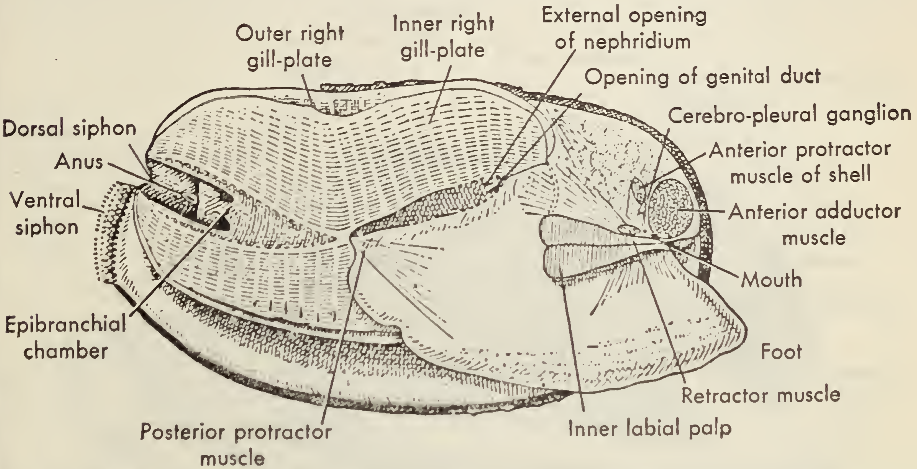


Fig. 25:12 *Anodonta mutabilis*, right side, with mantle cut away and right gills folded back. After Shipley and MacBride, from Hegner, *College Zoology*, The Macmillan Company.

The cilia cause water to enter at the incurrent siphon and pass out at the excurrent siphon.

The internal organs (Fig. 25:13) are imbedded in a solid mass of which the foot constitutes the ventral portion. The **mouth** opens into the mantle cavity just under the anterior adductor muscle. A short **esophagus** leads into the **stomach,** which in turn leads into a long, coiled **intestine.** The **coelom** is reduced to a single cavity, the **pericardial cavity** surrounding the heart, which lies dorsal to the other organs. The intestine passes through this cavity and through the heart before opening by the **anus** into the posterior dorsal portion of the mantle cavity near the origin of the excurrent siphon. The excretory organs consist of one pair of modified **nephridia** opening on the one hand into the coelom surrounding the heart and on the other hand into the mantle cavity. The **heart** pumps the blood through **arteries** to the various organs of the body from which it is returned to the heart by **veins.** The system, however, is an open one, there being no capillaries as in vertebrates. The nervous system consists of three ganglia connected by nerve cords: a **cerebro-pleural ganglion** ventral to the stomach just where the esophagus joins it, a **visceral ganglion** ventral to the posterior adductor muscle, and a **pedal ganglion** in the foot. Near the mouth are the labial palps, the function of which seems to be to taste water entering by the incurrent siphon. Near the pedal ganglion is an organ of equilibrium.

The sexes are separate. The gonads lie in the tissue surrounding the coils of the intestine. The eggs are extruded through a short oviduct into the mantle cavity where they are fertilized by sperms from another mussel carried in the current of water entering by the incurrent siphon.

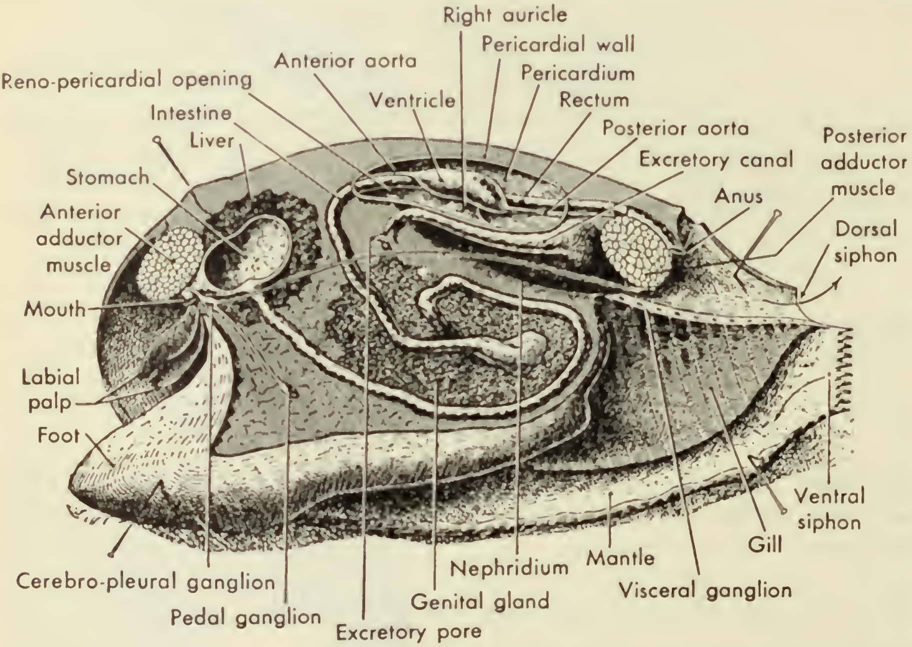


Fig. 25:13 Internal organs of a mussel. The cerebro-pleural ganglion is here called the brain. After Jammes, from Hegner, *College Zoology*, The Macmillan Company.

The eggs hatch out into a peculiar kind of larva called a **glochidium** (Fig. 25:14). A glochidium resembles an adult mussel in having two hinged valves which are closed by a muscle, but its mode of life is surprisingly different. In *Anodonta* the eggs are usually fertilized in August and the glochidia remain in the mantle cavity of the mother through the winter. In the spring they pass out into the water where, if they are fortunate, they become parasites on the skin or gills of fish. They attach themselves by catching hold with the two valves of their shells. The skin of the fish grows over the small parasites, forming "blackheads." In this position the young mussel leads a parasitic existence, obtaining its nourishment from the tissues of the fish for from 3 to 12 weeks, during which time it gradually metamorphoses into the adult form which drops off the fish and continues its life on the river or lake bottom. The parasitic stage of the fresh-water mussel is an adaptation for wider dispersal. By becoming attached to the fish it is carried to new feeding grounds. Not all bivalve mollusks pass through a parasitic stage. The oyster, for example, leads an independent existence throughout its life.

The classes of mollusks are characterized in Chap. 3. The phylum is of interest on account of its abundance in fresh and salt water and its long fossil record. It is of economic importance not only on account of the large number of edible species but also because it provides food for many other edible animals including many fishes.

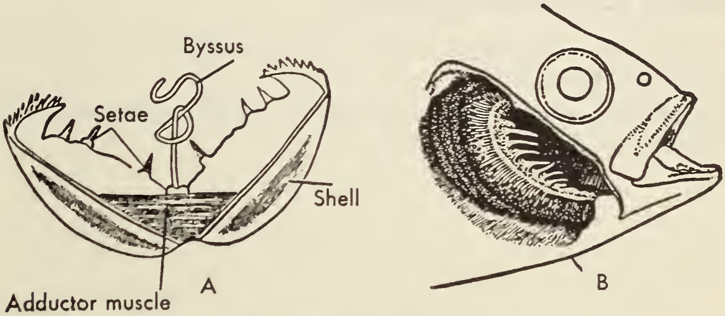


Fig. 25:14 A, a glochidium of a mussel; B, glochidia attached to the gills of a fresh-water fish. From Hegner, *College Zoology*, The Macmillan Company.

Topical Outline of Chapter 25

1. Review of the phyla already considered 491
2. Sponges (phylum Porifera) 493
3. Rotifers (phylum Rotifera) 495
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5. The lamp shells (phylum Brachiopoda) 497
6. Echinoderms (phylum Echinodermata) 497
7. Mollusks (phylum Mollusca) 500

Questions

1. Discuss the stages in evolution represented by the different phyla of animals so far studied.
2. Discuss the structure of a sponge. What three different kinds of skeletons are found in sponges? Just what is a "bath sponge"?
3. Describe briefly the skeleton of a starfish.
4. How does a starfish move?
5. How does a starfish feed?

6. Describe the skeleton of a clam. How is it kept closed?
7. What is to be seen in the mantle cavity of a clam?
8. Describe the digestive system of the clam.
9. What is peculiar about the relation between the heart and digestive system of the clam?
10. Trace the life history of a fresh-water mussel.
11. What are the characteristics of the three chief classes of mollusks and what common animals does each class include?

Suggestions for Further Reading

Hegner, Robert W., *Invertebrate Zoology*, The Macmillan Company, New York, 1933, Chaps. IX and XI.

Buchsbaum, Ralph, *Animals without Backbones*, The University of Chicago Press, Chicago, 1938, Chaps. 17 and 18.

PART IV. Vertebrate Anatomy and Physiology Based on the Frog and Man

"The process of digestion, as I have been informed by anatomical friends, is one of the most wonderful works of nature. I do not know how it may be with others, but it is a great satisfaction to me to know, when regaling on my humble fare, that I am putting in motion the most beautiful machinery with which we have any acquaintance."

Charles Dickens

CHAPTER 26

The Vertebrates

Vertebrates are our most familiar animals and include all the various kinds of fishes, frogs, salamanders, reptiles, birds, and mammals. They are the most highly organized of all animals and dominate the land, the air, and the sea. Reasons for their success will become apparent by comparing them with invertebrates and the comparison will serve also to bring out the distinguishing characteristics of vertebrates.

1. A COMPARISON OF VERTEBRATES AND INVERTEBRATES

Two characteristics distinguish at a glance most vertebrates from invertebrates. (**Invertebrate** is a general term used to designate all animals which are not vertebrates.) All typical vertebrates have two pairs of appendages (fins or legs), while invertebrates, if they have appendages at all, usually have several pairs. Although the body of a vertebrate may be more or less enclosed in a protective covering of scales (fishes) or horny plates (reptiles), the supporting **skeleton** is internal and consists of cartilage or bone, both of which materials contain living cells and are capable of growth and modification during life. On the other hand, the supporting skeleton of invertebrates, when one is present, consists of a secretion of the epidermis (arthropods, mollusks, and coelenterates), or of a series of interlocking mesodermal plates (echinoderms) or spicules (sponges). In the case of the arthropods growth of the animal is possible only by casting off the exoskeleton and secreting a new one. In mollusks growth of the shell occurs only in thickness and at the margin. In echinoderms continuous growth of the skeleton occurs and in this respect these animals resemble vertebrates.

In the soft parts the striking and important differences are in the nervous and respiratory systems. The **nervous system** of a vertebrate consists of a long tube extending the length of the body, enlarged in the head to form the brain. This nervous or neural tube lies in the neural canal of the vertebral column and is formed in the embryo from an infolding of the outer cell layer of ectoderm and lies dorsal to the notochord. In the adult the walls of this tube become much thickened and contain numerous nerve cells, from which nerve fibers go to the various parts of the body. The invertebrate nervous system is built on an entirely different plan. It consists, in the higher invertebrates, of a series of solid ganglia all of which, with the exception of the most anterior pair (most invertebrates) or pairs (some insects), are ventral to the digestive tract.

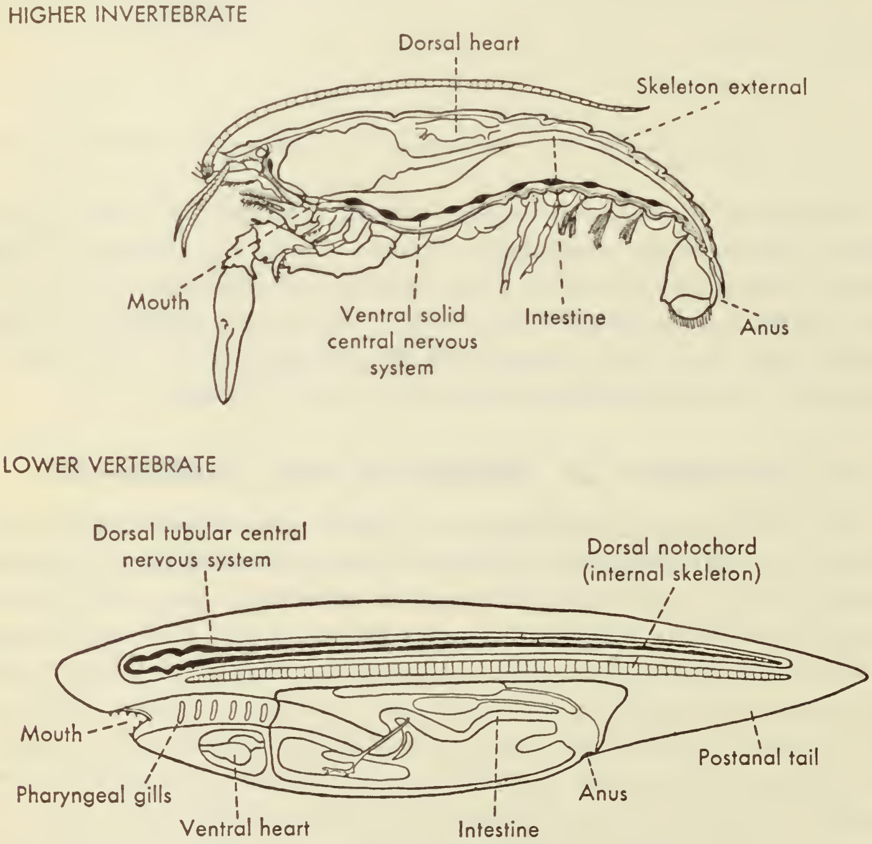


Fig. 26:1 A higher invertebrate contrasted with a lower vertebrate.

In the higher invertebrates the **respiratory organs** are usually formed from the external cellular layer of the body or ectoderm, either as outgrowths (most aquatic forms) or as ingrowths (insects which are typically land forms). In insects fine air tubes or tracheae ramify among the cells of the tissues and oxygen passes to and carbon dioxide from the different parts of the body largely by diffusion through these tubes. The respiratory organs of vertebrates are developed from the endodermal lining of the pharynx. In fishes they consist of gills associated with gill clefts opening from the pharynx to the exterior, breathing being accomplished by taking water into the mouth and passing it out over the gills and through the gill clefts. In reptiles, birds, and mammals, lungs are developed from the floor of the pharynx and breathing is accomplished by passing air in and out of these sacs. However, gill clefts appear in the embryos of even those vertebrates (reptiles, birds, and mammals) which are without functional gills.

In most of the higher invertebrates the **vascular system** is an open one, i.e., the blood is not confined to blood vessels but passes into a space or spaces in the body called a **hemocoel.** In vertebrates the blood is confined to arteries, capillaries, and veins and circulates along definite paths. The heart or other pumping organ of invertebrates is usually dorsal to the digestive tube. In vertebrates it is ventral and anterior. The respiratory pigment, i.e., the substance which combines with oxygen and aids in its transport to the tissues, when present in invertebrates is dissolved in the plasma of the blood. In vertebrates the respiratory pigment, which is **hemoglobin,** is contained in the red corpuscles.

The accompanying table (Table 26:1) summarizes the differences in structure between vertebrates and higher invertebrates (Fig. 26:1).

TABLE 26:1. COMPARISON OF INVERTEBRATES AND VERTEBRATES

	HIGHER INVERTEBRATES	VERTEBRATES
Appendages	If present, usually several pairs	Typically two pairs, never more than two
Skeleton	Usually external and formed as a secretion of the ectoderm. Does not contain living cells	Internal. A notochord in the embryo partly or completely replaced in the adult by a vertebral column and appendicular skeleton of cartilage or bone which contains living cells
Nervous system	Solid ganglia connected by nerve fibers to form a chain, the main portion of which is ventral to the digestive tract	A hollow tube, dorsal to the notochord or centra of the vertebral column and enlarged anteriorly to form a brain
Respiratory system	Usually developed from the ectoderm, varies greatly in the different phyla	Developed in relation to the wall of the pharynx and consists of either gills or lungs, gill clefts present in the embryos of all vertebrates
Circulatory system	Usually not a closed system, the blood passing into a hemocoel. The heart when present is dorsal. The respiratory pigment is dissolved in the plasma of the blood	A closed system with arteries, veins, and capillaries. The heart is ventral and anterior. The hemoglobin of the blood is contained in red blood corpuscles

2. HOW THE VERTEBRATE TYPE OF STRUCTURE HAS SOLVED SOME PROBLEMS

How have these structural features contributed to make the vertebrates a successful group by solving the major problems which confront an animal living in water, on land, or in the air? It seems probable that the restriction of the appendages to two pairs, as occurs in vertebrates, has been an important contributing factor to the development of the anterior end of the neural tube into a dominant brain. The tubular type of central nervous system combined with the reduced number of appendages seems to be particularly adapted to the development of the type of nervous system which shows less stereotyped and more varied reactions.

Vertebrates have solved the problem of support for their soft parts by developing an internal or endoskeleton which can be added to or subtracted from as the growth of the animal requires without interrupting its activities. The growth and absorption of bone and cartilage is possible because they contain living cells which build up or break down the skeletal material. In their dorsal position in vertebrates the brain and spinal cord are protected and isolated from the movements and other changes which go on in the organs of the abdominal cavity. Being ventral and anterior, the heart is near the respiratory organs and removed from the nervous system which might be disturbed by its constant activity. The development of the respiratory organs from the pharynx brings them close to the heart. In this position they are well situated to receive blood directly from the heart and to aerate it previous to its distribution to the various organs of the body. A closed vascular system provides for a more rapid and complete circulation of the blood. The red blood corpuscle with its contained hemoglobin is a much more efficient carrier of oxygen than the invertebrate blood. Other features which have contributed to the success of the vertebrates, especially the higher forms, will be discussed in the chapters which follow.

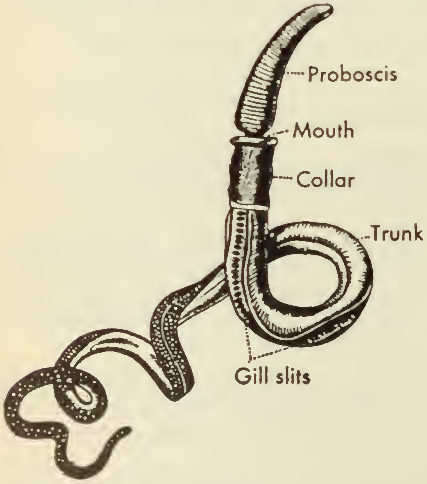


Fig. 26:2 *Dolichoglossus kowalevskii* (subphylum Hemichordata), a protochordate related to *Balanoglossus*. After Shipley and MacBride, from Hegner, *College Zoology*, The Macmillan Company.

3. THE PHYLUM CHORDATA

Although a large and important group, the vertebrates do not constitute a phylum, but the subphylum Vertebrata. The phylum Chordata to which the subphylum Vertebrata belongs includes three other subphyla which are sometimes grouped together as the **protochordates.** These latter include a number of inconspicuous and unfamiliar small animals which are nevertheless of considerable interest since they show possible stages through which the ancestors of the vertebrates may have passed.

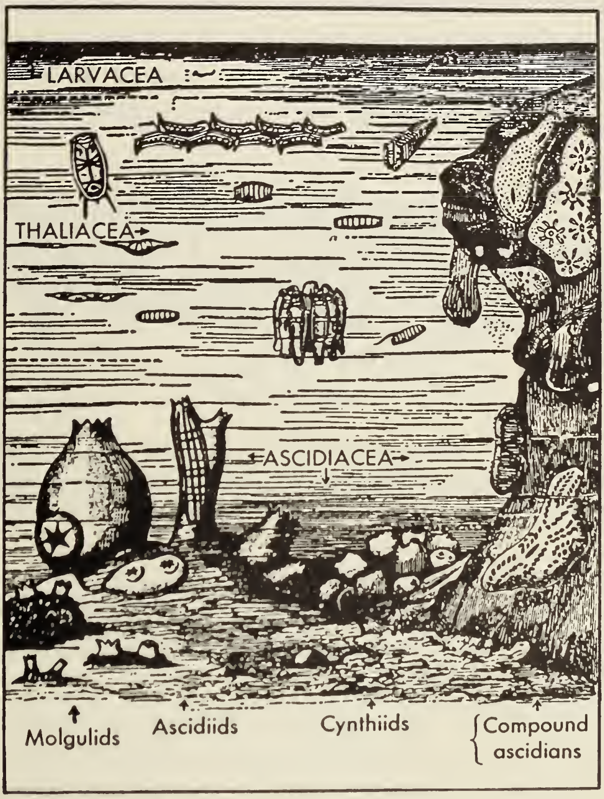


Fig. 26:3 Sketch of the chief kinds of urochords (subphylum Urochordata), found in the sea. After *Cambridge Natural History*, from Hegner, *College Zoology*, The Macmillan Company.

The phylum Chordata is distinguished by the presence, at some stage in the development of the individual, of a notochord, pharyngeal gill slits, and a hollow dorsal nervous system. A **notochord** is a more or less rigid rod of cells, extending longitudinally in the dorsal part of the body, ventral to the central nervous system and dorsal to the digestive tube.

Three subphyla are usually included in the **protochorda.** They are the Hemichorda, Urochorda, and Cephalochorda. The **Hemichorda** (Gr. *hemi*, half + L. *chorda*, cord) are wormlike marine animals. The best known genera, *Balanoglossus* and *Dolicoglossus*, burrow in the sand of the seashore just below low tide. The body is divided into proboscis, collar, and trunk (Fig. 26:2). The **proboscis** is a burrowing organ which forms the anterior end of the animal. The **notochord** is confined to the proboscis region. The **mouth** is on the ventral side between the proboscis and the collar. The **collar** is a relatively short region surrounding the anterior end of the alimentary tract. The **central nervous system** is a hollow tube extending through the dorsal portion of the collar. The **trunk** makes up most of the length of the body and contains the pharynx and intestine. **Pharyngeal gill chambers** open individually to the exterior by a series of clefts on either side of the anterior portion of the trunk (pharyngeal portion).

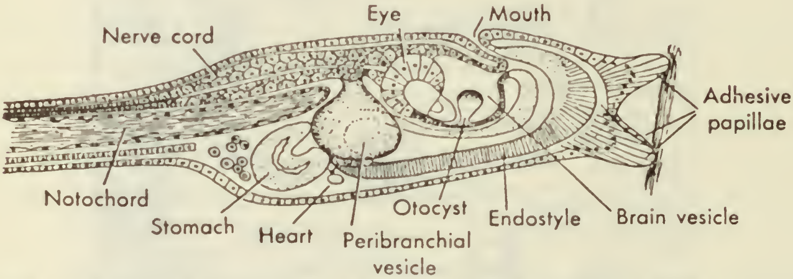


Fig. 26:4 The larva of a urochord. A diagrammatic longitudinal section through the body. The atrium has here been labeled peribranchial vesicle. After Delage et Herouard, *Traité de Zoologie Concrète*, from Wolcott, *Animal Biology*, McGraw-Hill Book Company, Inc.

The **Urochordata** (Gr. *oura*, tail) are also known as tunicates, ascidians, and sea squirts. The adult animals are fairly common in the ocean and are either free swimming or attached (Fig. 26:3). But, from the point of view of the evolution of the vertebrates, the **larval stage** (Fig. 26:4) is more interesting than the adult in which most of the chordate characters are lost. In external appearance the larva resembles a small frog tadpole, and, like the latter, the urochord tadpole is without paired appendages. The **notochord** is in the tail of the larva and is lost in the adults of the attached forms. There is a **dorsal nervous system** which in the larva is hollow and includes a relatively large **brain vesicle.** Respiration is by means of **pharyngeal gills,** the clefts of which do not open directly to the exterior but into an ectoderm-lined cavity called the **atrium,** surrounding the pharynx and communicating with the exterior by a single opening.

The **Cephalochorda** (Gr. *kephale*, head) are small fishlike animals which live in the sand of the seashore just below low tide. They are not common animals and are represented by only a few genera found in certain parts of the world in the tropics and subtropics. The best known is *Amphioxus* (Gr. *amphi*, both + *oxus*, sharp) which externally resembles a small fish but lacks a distinct head and is without paired appendages (Fig. 26:5). The **notochord** extends throughout the entire length of the body and persists throughout life. The **central nervous system** is a hollow thick-walled tube, extending through almost the entire length of the animal, the cavity of which (but not the walls) is enlarged anteriorly to form a **brain vesicle.** There are no paired eyes or ears. There is a respiratory pharynx with numerous **gill clefts** which open into an **atrium** surrounding the anterior half or two-thirds of the body on the ventral side and opening to the exterior, posteriorly, by a single pore. There is no distinct heart.

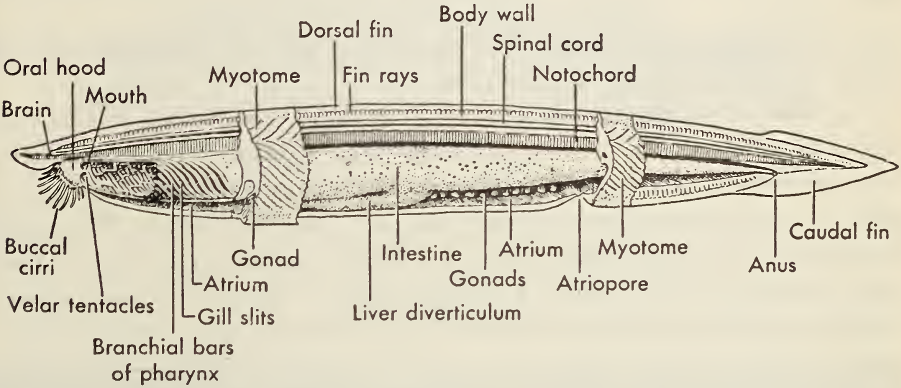


Fig. 26:5 Diagram of a dissection of *Amphioxus* (subphylum Cephalochordata) to show the main features of its anatomy. From L. L. Woodruff, *Animal Biology*, The Macmillan Company.

4. THE CLASSES OF VERTEBRATES[1]

The vertebrates naturally fall into five groups: fishes, amphibians, reptiles, birds, and mammals. The last four groups are recognized as classes and named accordingly class Amphibia, class Reptilia, class Aves, and class Mammalia. The animals we think of as fishes do not form a single class. Living fishes are grouped into three classes: the Cyclostomata, the Chondrichthyes, and the Osteichthyes.

The **Cyclostomata** (Gr. *cyclos*, round + *stoma*, mouth) are the most

[1] For a systematic classification of the vertebrates see the Appendix.

primitive of vertebrates. They have round, sucking mouths without jaws, numerous gill clefts, no paired appendages, and a poorly developed skull. The sea lamprey (Fig. 26:6) inhabits the Atlantic coasts of North America, Europe, and Africa. It seeks fresh water to spawn, and in the spring ascends rivers for this purpose.

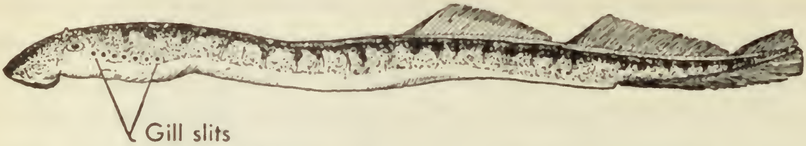


Fig. 26:6 A cyclostome, the lamprey, *Petromyzon marinus* (subphylum Vertebrata, class Cyclostomata). After Deen, from L. L. Woodruff, *Animal Biology*, The Macmillan Company.

The **Chondrichthyes** (Gr. *chondros*, cartilage + *ichthyus*, a fish) are, with a few exceptions, medium or large-sized marine fishes (Fig. 26:7). Their skeleton is of cartilage or gristle. The brain is enclosed in a cranium to which the upper and lower jaws are loosely attached. The scales consist of bony plates which bear teethlike enamel projections. These projections give to the surface a rough sandpaperlike feeling and, indeed, the dried skin of these fishes is used in place of sandpaper in certain parts of the world. The mouth opening is usually on the under side. The gill clefts, which are usually five on each side, open directly to the exterior. There are two pairs of lateral fins. Included in this class are the dogfishes, sharks, and rays.

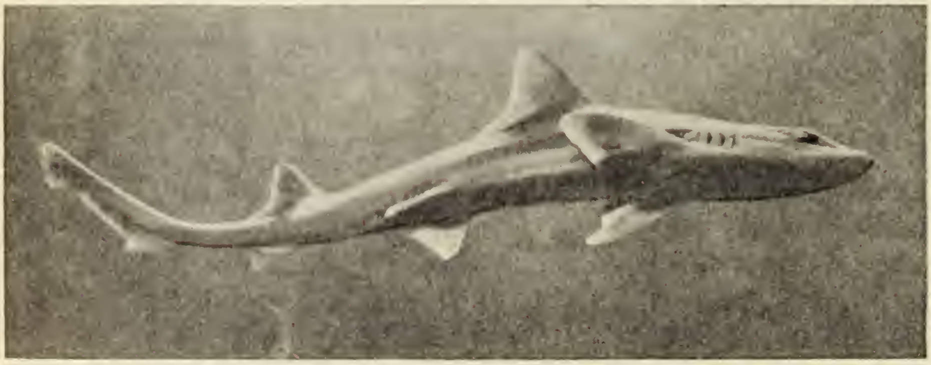


Fig. 26:7 A common dogfish, *Mustelus* (class Chondrichthyes). Note the gill clefts. Photograph by J. W. Mavor.

In the **Osteichthyes** (Gr. *osteon*, bone + *ichthyus*, fish) the skeleton is composed, at least in part, of bone. In most of these fishes the scales consist of thin bony plates which are arranged so that they overlap and are covered by the epidermis. On each side of the head is a bony plate, the **operculum,** which projects backward and protects the gills.

The living Osteichthyes are divided into three subclasses, the **Actinopterygii** (Gr. *actis*, *actinas*, a ray + *pteryx*, *pterygos*, a fin) or ray-finned fishes, the **Dipnoi** (Gr. *di*, twice + *pnoe*, breath) or lungfishes, and the **Crossopterygii** (Gr. *crossoi*, a fringe + *pteryx*, *pterygos*, a fin) or lobed-finned fishes. Most living fishes with the exception of the sharks and rays belong to the order **Teleostei** (Gr. *teleos*, complete + *osteon*, bone) which is a branch of the subclass Actinopterygii.

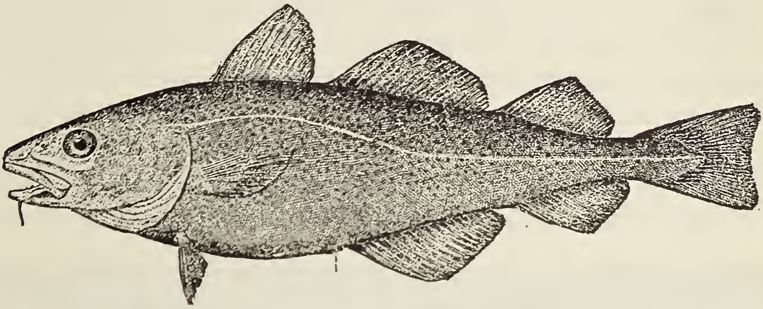


Fig. 26:8 The cod, *Gadus callarias* (class Osteichthyes, subclass Actinopterygii, order Teleostei). After Goode, from Hegner, *College Zoology*, The Macmillan Company.

The variety in size, structure, color, and habits of the teleostean fishes is rivaled only by that of birds. They range, in size, from a small tropical fish less than ½ inch in length to the giant tarpon or tuna or sailfish (Fig. 3:23); in shape, from the long slender eel or pipefish to the "sawed-off" sunfishes; in color, from the drab codfish (Fig. 26:8) to the beautifully colored fishes of the tropics; in habits, from the peculiar fish that deposits her eggs in the mantle cavity of a clam where they develop as parasites, to the deep-sea fish that lures its prey with a luminescent bait.

The lungfishes, or Dipnoi, are of particular interest because they indicate how the next class of vertebrates, the amphibians, may have been developed from fishes. Of these fishes, once numerous, there are now only three existing genera, the Australian lungfish, *Neoceratodus fosteri* (Fig. 26:9), the central African lungfish, *Protopterus* and the South American lungfish, *Lepidosiren*. In each of these there is an air bladder which opens into the pharynx and functions as a lung. Lungfishes live

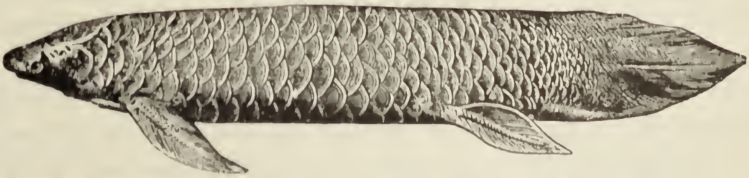


Fig. 26:9 The Australian lung fish, *Neoceratodus fosteri* (class Osteichthyes, subclass Dipnoi). After Gunther from Hegner, *College Zoology*, The Macmillan Company.

in stagnant pools or swamps where the water lacks oxygen. The African lungfish is able to survive the dry season when the marshes dry up by burrowing in the earth and breathing air. Although all of the living lungfishes are included in the subclass Dipnoi, lungs were also developed in the subclass Crossopterygii, a group of fossil fishes differing somewhat from the Dipnoi. The lobed fins of the Crossopterygii bear more resemblance to the limbs of land vertebrates than do the fins of the other fishes and this group is therefore thought to be nearest the direct line of descent of the higher forms. Very recently, 1939, a fish was caught off the coast of South Africa which seems to be a living representative of the Crossopterygii, although it probably did not breathe with lungs.

The class **Amphibia** (Gr. *amphibios*, living a double life) includes the frogs (Fig. 27:1) and salamanders (Fig. 26:10). The name "Amphibia" refers to the fact that many of these animals lead a kind of double life, partly aquatic and partly terrestrial. The larvae, usually called **tadpoles,** are always aquatic and breathe by means of gills. Lungs are developed in most species. And the adults, even when they spend their entire existence in the water, breathe air. In some species, e.g., the mud puppy, *Necturus* (Fig. 26:10), both gills and lungs are found in the adult. In nearly all cases their eggs are laid in water so that even those which leave the water for a part of their lives return to it in the breeding season. The appendages of amphibians are adapted for crawling rather than swimming and are built on the same plan as those of the higher groups of Vertebrates. The surface of the body is smooth and slippery and without scales, except in certain legless tropical forms. Like the members of the previous three classes, the Amphibia are cold blooded. In regions where the temperature in winter goes below freezing the Amphibia burrow into the mud at the bottom of ponds and marshes where they hibernate in a dormant condition awaiting the coming of spring and warmer weather.

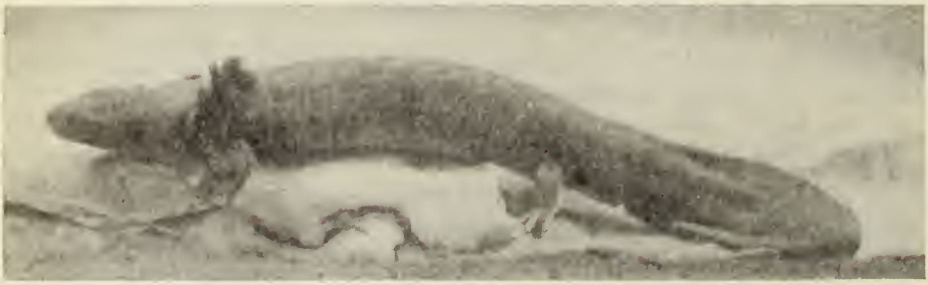


Fig. 26:10 *Necturus* (class Amphibia), an amphibian with gills in the adult. From a photograph provided by the John G. Shedd Aquarium, Grant Park, Chicago, Ill.

The class **Reptilia** (L. *repere*, to creep) includes lizards (Fig. 39:10), snakes (Fig. 39:30), turtles (Fig. 3:25), tortoises, crocodiles, alligators, and numerous bizarre extinct forms such as the dinosaurs and pterodactyls. Reptiles are land animals, although a few, like the turtles and crocodiles and the ancient ichthyosaurs, have secondarily taken to water. Although gills are present in the embryo, they are never functional. When hatched the young breathe air through lungs. Their bodies are covered with horny scales formed from the outer layer or epidermis of the skin. Reptiles, like amphibians, are cold blooded and those which live in regions where the temperature goes below freezing go through a period of hibernation. Although once the dominant group of animals upon the earth, reptiles are now rapidly becoming extinct, chiefly at the hands of man.

All birds belong to the class **Aves** (L. *avis*, a bird). No one has any difficulty in recognizing a bird. Its feathers are unique. They are really modified and embellished scales. The fore limbs are adapted to flight (Fig. 26:11). Some fossil birds had teeth like reptiles, but in all living birds their place is taken by a horny covering or beak. All birds develop from eggs and are warm blooded, that is to say, their bodies are maintained at a relatively constant "warm" temperature. This higher temperature enables them to control their metabolic processes to an extent not possible for either amphibians or reptiles and to live and remain active in regions where the temperature goes below freezing. Living birds are classified in two divisions: the Ratitae, which includes only a few species such as the wingless apteryx of Australia and the ostrich, and the Carinatae or keeled birds, which includes all other living birds. Birds are of great interest from many points of view, but it is beyond the scope of this text to go into the various aspects of this special-

Fig. 26:11 A sea gull (class Aves, division Carinatae) about to dive for a fish. Photograph by Dr. E. G. Evans, reproduced by permission of Carl Zeiss, New York.

ized group; however, a somewhat detailed classification is given in the appendix.

Mammals (Fig. 3:29), which compose the class **Mammalia** (L. *mamma*, breast), are characterized by being covered with **hair,** which takes the place of the scales of reptiles, and by feeding their young with a secretion called **milk** formed in glands called **mammary glands** which are developed in the skin of the ventral side of the body. In all except two very primitive forms, the duckbill and the spiny "anteater" which lay eggs, the young are born alive and are like their parents. The mammals are all warm-blooded and active animals, although some, like the brown bear, may hibernate in winter.

5. THE SUBCLASSES OF MAMMALS

The class Mammalia is divided into three subclasses. The subclass **Prototheria** (Gr. *protos*, first + *therion*, beast) contains the two egg-laying mammals already mentioned. The subclass **Metatheria** (Gr. *meta*, between) contains the pouch-bearing mammals such as the opossum and the kangaroo. The subclass **Eutheria** (Gr. *eu*, complete) contains all other living mammals.

Considerable interest attaches to the three living genera of **Prototheria,** survivors of a geological age long past. The **duckbill** (*Ornithorhynchus*) (Fig. 3:27) is a woolly creature about the size of a large ground hog with short legs. The front feet are webbed and in the adult the teeth are replaced by horny pads giving the snout somewhat the appearance of a duck's bill or beak. The animal is confined to South Australia and the adjacent island of Tasmania. It is aquatic and lives on insects, worms, and small crustaceans. There are two genera of **spiny anteaters,** *Echidna* and *Proechidna*. They are of about the same size as the duckbill but differ in appearance and habits. Among the hairs of the back are numerous long spines. The head is extended into a long, tubular snout on the end of which is the small mouth. Their food consists of ants which they obtain by burrowing underground. They are confined to Australia, Tasmania, and New Guinea.

The duckbill and the spiny anteaters lay eggs. The egg of the duckbill is about $\frac{3}{4}$ inch in length and covered with a leathery shell; those of the spiny anteaters are about $\frac{1}{2}$ inch in length and have calcareous shells. The spiny anteater places its single egg, as soon as laid, in a fold of the skin of the abdomen which forms a pouch where it is incubated until hatched. The duckbill lays its two eggs and rears its young in a burrow underground. In both animals numerous ducts convey milk from the mammary glands to depressions on the surface of the abdomen, from which it is licked by the young.

The **Metatheria,** or **marsupials** as they are often called, bear their young alive but in a very immature state. The development is continued in the abdominal pouch or marsupium. In this pouch the young attach themselves to long teats. A specially developed structure connects the windpipe with the nasal cavity in the new-born animal and makes it possible for the mother to force milk through the teat and into the esophagus without interrupting its breathing. The Metatheria are all confined to Australia, Tasmania, New Guinea, and the near-by islands, except for the different species of American opossums. In Australia the Metatheria largely take the place occupied by Eutheria elsewhere in the world. There are marsupial "cats," "wolves," "otters," "moles," "rabbits," "anteaters," and the peculiar kangaroo (Fig. 3:28).

The **Eutheria,** or, as they are often called, **placental mammals,** are the dominant group of mammals, indeed of land animals, today (Fig. 3:29). The young are nourished during their intra-uterine life by a **placenta** and are born alive. The placenta is a vascular and protective structure formed partly from tissues contributed by the embryo and partly from tissues contributed by the mother. In the placenta the blood of the mother surrounds blood vessels from the embryo, without there being any direct transfer of blood between the two organisms. The embryo receives its nourishment and oxygen from and gives its waste products to its mother by diffusion through the walls of the placental blood vessels. The placenta makes possible the prolonged and advanced development of the young eutherian mammal in the warm and protecting body of its mother.

6. THE ORDERS OF EUTHERIAN MAMMALS

A number of different orders of the Eutheria are distinguished. These show in most cases adaptations to different modes of life. We will consider only some of the more important of these.

The **Insectivora** (L. *insectum*, insect + *vorare*, to devour) include the hedgehogs, moles (Fig. 26:12), and shrews which feed almost entirely on insects or worms. They are regarded as probably the most primitive of the living Eutheria.

The **Chiroptera** (Gr. *cheir*, hand + *pteron*, wing) are the animals commonly called bats (Fig. 26:13). The fore limbs, and to some extent the whole body, is modified for flight. The bones of the fingers are greatly elongated and a fold of skin extends between them, the body, and the

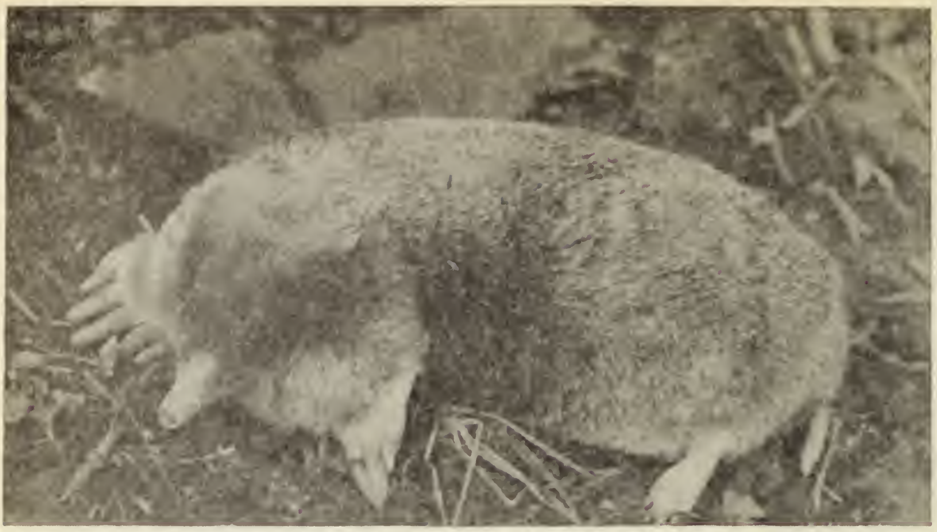


Fig. 26:12 A common mole, *Scalopus* (class Mammalia, subclass Eutheria, order Insectivora). Note the large forefeet adapted for digging. Photograph by L. W. Brownell.

hind legs, forming wings. Bats are mainly of three types which feed, respectively, on fruit, insects, and the blood of warm-blooded animals. Contrary to popular belief, the latter type, known as vampire bats, are small animals.

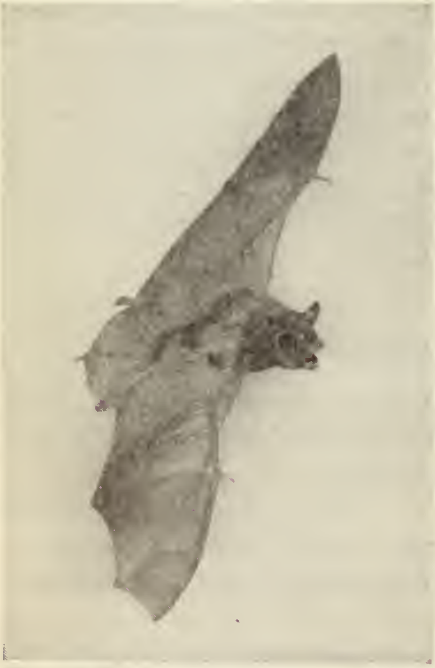


Fig. 26:13 A small brown bat, *Myotis* (class Mammalia, subclass Eutheria, order Chiroptera) in flight. High-speed photograph by Harold E. Edgerton.

The **Carnivora** (L. *caro*, *carnis*, flesh + *vorare*, to devour) are the carnivores or flesh-eating mammals. Their feet have claws and their teeth are sharp and adapted to tearing flesh. The order contains a large number of species and many animals familiar to the hunter or the visitor to the zoo. One large family contains the cats, lions (Fig. 3:29), tigers, leopards, lynxes, jaguars, and pumas. Another contains the dogs, wolves, and foxes. Yet another contains many of our fur animals, the weasels, badgers (Fig. 39:19), minks, ermines, ferrets, skunks, and otters. The Carnivora are believed to be a primitive group which may have given rise to more specialized groups.

The **Pinnipedia** (L. *pinna*, fin + *pes*, *pedis*, foot) include the seals and their relatives, the sea lion and the walrus. These animals resemble carnivores and are sometimes included in the same group. They differ from them chiefly in that their limbs are paddle-shaped (Fig. 26:14).

The order **Primates** (L. *prima*, *primates*, one of the first) contains the lemurs, monkeys, apes (Fig. 26:15), and man. This order is often put at the end of the list, chiefly because it includes man. However, the group as a whole is not so specialized as the other orders which follow in this list. The chief characteristics of the order are: nails take the place of claws on the digits; the first digit (thumb) opposes the others; the eyes are directed forward; and the brain is relatively large. Lemurs are small, furry, arboreal animals with long tails. They are most abundant in Madagascar but are found also in tropical Africa and some of the islands of the East Indies. The zoological position of the apes and man is discussed in some detail in Chap. 44.

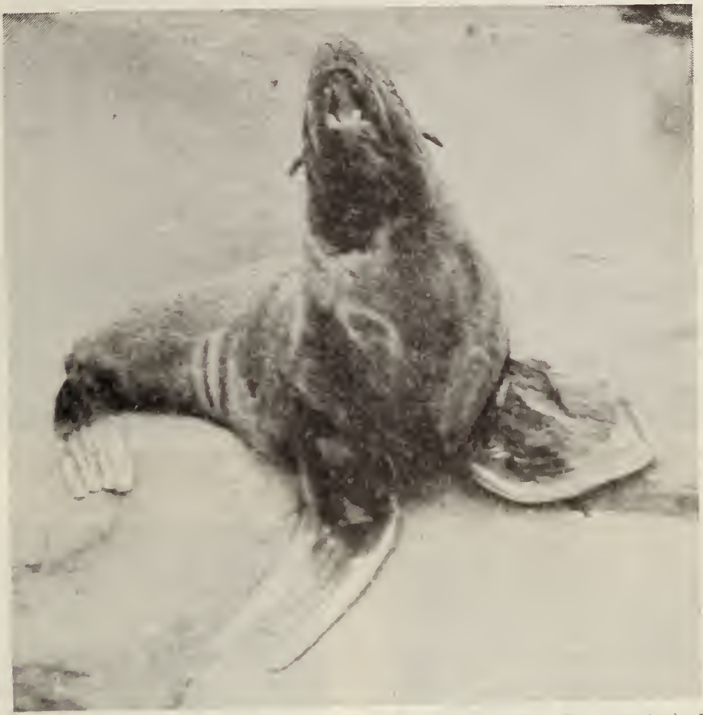


Fig. 26:14 A seal (class Mammalia, subclass Eutheria, order Pinnipedia). Photograph by J. W. Mavor.

The **Edentata** (L. *e*, without + *dens*, *dentis*, tooth) include a few mammals which are the remnants of a much larger and more widely distributed group of prehistoric times. The name, which means "without teeth," is

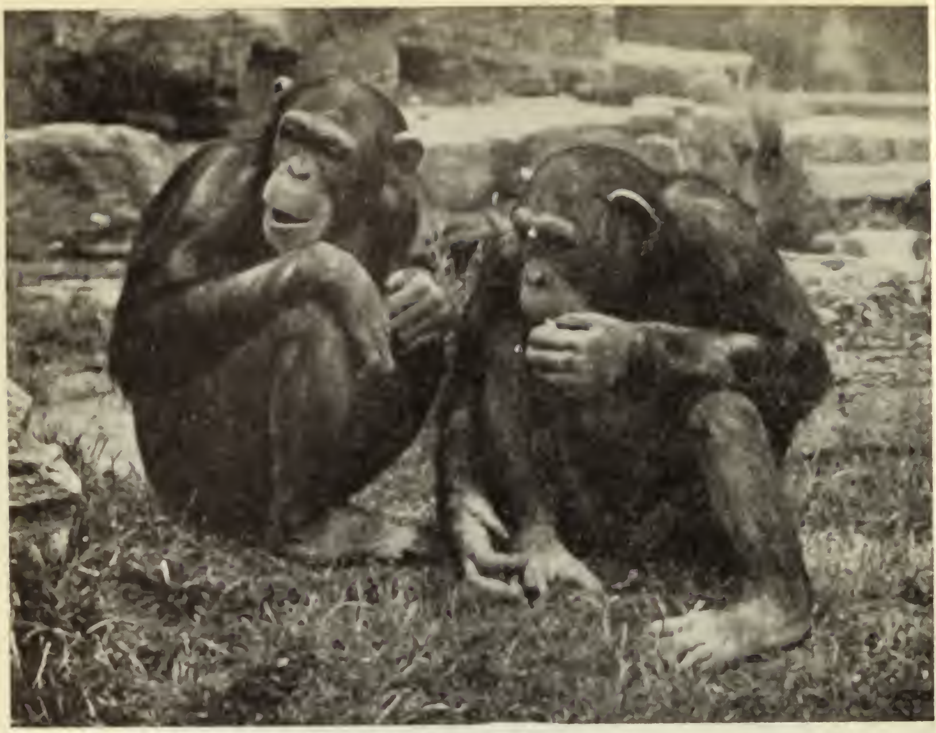


Fig. 26:15 Chimpanzees, *Pan* (class Mammalia, subclass Eutheria, order Primates). Photograph by J. W. Mavor.

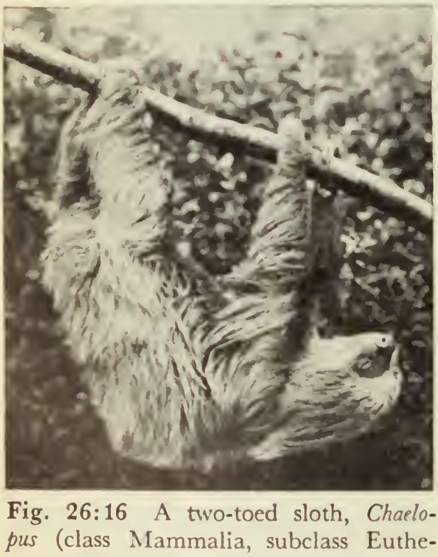


Fig. 26:16 A two-toed sloth, *Chaelopus* (class Mammalia, subclass Eutheria, order Edentata). Photograph reproduced by permission of the National Zoological Park, Washington, D. C., a branch of the Smithsonian Institute.

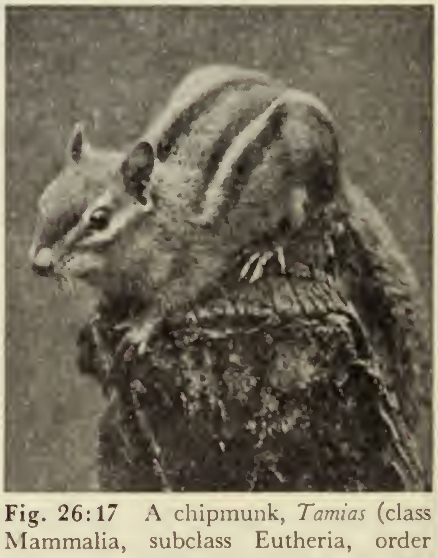


Fig. 26:17 A chipmunk, *Tamias* (class Mammalia, subclass Eutheria, order Rodentia). Photograph by L. W. Brownell.

not entirely appropriate since many of them have teeth. However, the teeth are imperfect and without enamel. The order is confined mainly to South America and includes the American anteater, the sloths (Fig. 26:16), and the armadillos.

The **Pholidota** (Gr. *pholis*, scale + *osis*, condition) are a small group consisting of the scaly anteaters or pangolins which are covered with pointed scales. They are confined to Africa and the Orient.

The **Rodentia** (L. *rodare*, to gnaw) are gnawing mammals and have two long chisellike front teeth in each jaw. Most of them are small terrestrial animals. This order contains more species than any of the other orders. It includes mice (Fig. 39:11), rats, chipmunks (Fig. 26:17), squirrels (Fig. 39:12), woodchucks, muskrats (Fig. 39:27), beavers, and porcupines.

The **Lagomorpha** (Gr. *lagor*, a hare + *morphe*, form) consist of the rabbits and hares which differ from the rodents in having four upper incisors instead of two. They are sometimes included in the Rodentia.

The **Hyracoidea** (Gr. *hyrax*, a shrew mouse) are represented by only a single living genus of small rodentlike mammals known as conies. They are peculiar in having only four digits on the fore limbs and three on the hind limbs.

The hoofed mammals or **ungulates** are divided into two orders: the Perissodactyla, or odd-toed ungulates, and the Artiodactyla, or even-toed ungulates.

The order **Artiodactyla** (Gr. *artios*, even + *dactylos*, toe) includes pigs, hippopotamuses, camels, sheep, goats, oxen, bison (Fig. 39:23), giraffes, and deer (Fig. 39:13). The number of toes is also reduced but the axis of the foot passes between the third and fourth digits. Deers, pronghorn antelopes, and all the animals belonging to the ox family (Bovidae) which includes sheep, goats, and oxen are ruminants, i.e., they chew the cud.

The order **Perissodactyla** (Gr. *perissos*, odd + *dactylos*, toe) includes tapirs, rhinoceroses, and horses (Fig. 42:2). The number of toes is reduced but the axis of the foot always passes through the third digit. The tapir has four toes on the fore feet and three on the hind feet. The rhinoceros has three toes on each foot. Living horses including zebras and asses (genus *Equus*) have a single toe on each foot.

The **Proboscidea** (Gr. *pro*, before + *boskein*, to feed) are represented among living mammals by the elephants and, in the recent past, by the mammoths and mastodons (Fig. 40:12). The feet have the form of circular pads where they touch the ground but each, nevertheless, contains five toes as indicated externally by five small hoofs. The body is covered with a thick loose skin with little hair. Characteristic is the long muscular proboscis at the end of which are the nostrils. The tusks are modified incisors. The grinding teeth at the back of the jaws are large and have complicated ridges.

The **Sirenia** (Gr. *seiren*, a sea nymph) consist of the manatees or sea cows. They are large aquatic herbivorous mammals and have broad crushing teeth. The fore limbs are finlike and the hind limbs are absent. The tail is rounded.

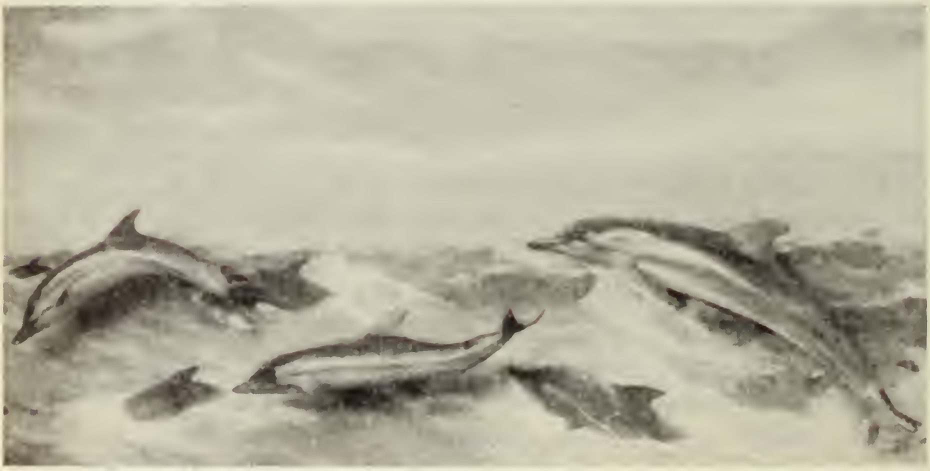


Fig. 26:18 Dolphins (class Mammalia, subclass Eutheria, order Cetacea) leaping through ocean waves. Photograph of a mural in the American Museum of Natural History, New York.

The **Cetacea** (Gr. *cetus*, a whale) are highly specialized aquatic mammals. The order includes the whales, porpoises, and dolphins (Fig. 26:18). The fore limbs are modified to form finlike paddles, the hind limbs are absent, and the tail forms a transverse fluke. The body is fish-shaped and covered under the skin with a layer of fat called blubber which acts as a heat insulator and enables the animals to maintain a relatively high constant temperature even in cold water. The young, as in all eutherian mammals, are born alive and nourished on milk produced by mammary glands. The sulphur-bottom whale is probably the largest animal known, living or extinct, and is said to reach a length of nearly 100 feet and a weight of 150 tons.

Topical Outline of Chapter 26

1. A comparison of vertebrates and invertebrates 507
2. How the vertebrate type of structure has solved some problems 510

3. The phylum Chordata 511
4. The classes of vertebrates 513
5. The subclasses of mammals 518
6. The orders of eutherian mammals 519

Questions

1. How would you distinguish between a vertebrate and an annelid? A vertebrate and an arthropod?
2. What are the most striking differences in internal structure between vertebrates and invertebrates?
3. Compare a higher invertebrate and a vertebrate as regards: (*a*) skeleton, (*b*) nervous system, (*c*) respiratory system, and (*d*) circulatory system.
4. Which characteristics of vertebrates help to make possible their large average size?
5. Compare a protochordate: (*a*) with an arthropod and (*b*) with a vertebrate.
6. Name the classes of vertebrates and give their distinguishing characteristics.
7. Give a classification of mammals.
8. Why are the duckbill and the spiny anteaters regarded as the most primitive mammals?
9. How does the development of the Metatheria differ from that of the Eutheria?
10. Name seven orders of eutherian mammals and briefly characterize each order.

Suggestion for Further Reading

Newman, H. H., *The Phylum Chordata, Biology of Vertebrates and Their Kin*, The Macmillan Company, New York, 1939.

CHAPTER 27

External Features, Skeleton, Joints, Muscles, and Body Cavity

As examples of vertebrates we will study the frog, long a favorite laboratory type, and the human being, the animal with which we are most familiar. In studying the frog we must remember that the genus *Rana* (frog) did not come into existence for our convenience but rather that frogs, large and small, should swim, eat, and be merry after the manner of tailless amphibians.

1. EXTERNAL FEATURES OF THE FROG

The species of frog usually studied in this country is the leopard frog, *Rana pipiens.* Its smooth body, divided into head, trunk, and limbs, is well adapted to slip through the grass and dive into the water of the streams and ponds along the margins of which it lives. In its ordinary resting position (Fig. 27:1) on land the long hind legs are bent at the sides of the body in the form of a rather flat Z; the top of the Z against the body is the **thigh,** the slanting portion the **shank,** and the lower part on the ground the **foot.** The short front legs, bent in a way that we should characterize as bowlegged if they were not in front, support the body in a slanting position. In this attitude, although at rest, the frog is ready for a spring. When he jumps the Z becomes a straight line and the legs are straightened out behind. If he alights on land it is on his fore feet, which take up the shock; if he enters the water the legs are held close to the sides of the body so as to make a clean dive.

In the water the frog may come to rest either on the surface or at the bottom. On the surface he floats with just the top of his head above water and his legs spread out. In this position his **nostrils,** two openings near the tip of his nose, are exposed as are also the two large **eyes,** which in a frog are on the top of the head as they are in a crocodile or hippopotamus and for the same reason. In this position they can be used with a minimum of the body above water. The eyes of the frog look out on either side. Thus he sees a different picture with each eye. In this position the ears are under water. The frog's eardrum or **tympanum** is on the surface of its body, so that there is no external ear such as in mammals. In this floating position the frog is able to see a bird or other enemy approaching from above, and is able immediately to dive by moving its legs upward and its head down.

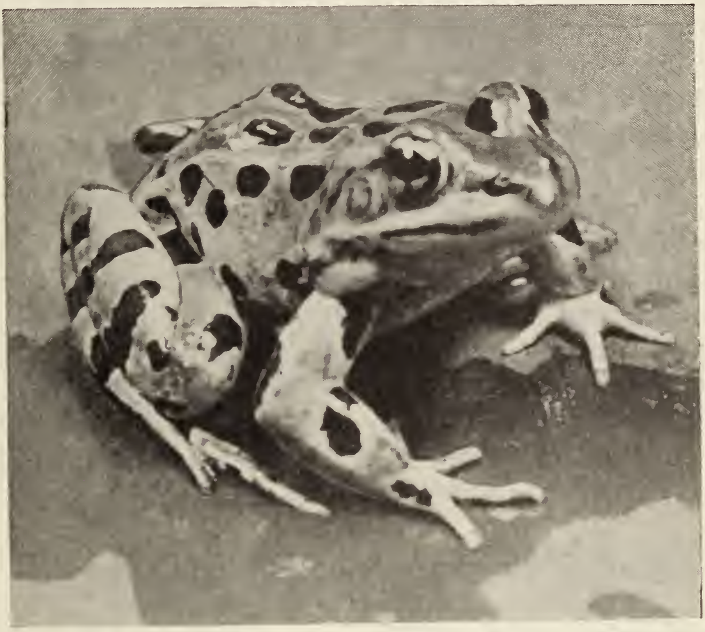


Fig. 27:1 A frog (*Rana pipiens*). Note attitude of the fore and hind limbs and the position of the nostrils, eyes, and eardrums. Photograph by J. W. Mavor.

The surface of the frog's body is smooth and covered with **mucus** secreted by glands in the skin. There are no claws upon its toes. Like the chameleon and many other lower vertebrates the frog has the **power to change color**. This is due to changes in black and yellow pigment cells, also in the skin. In all its external features the frog shows a high degree of adaptation to its life in the grass and shrubs along the margins of ponds and streams.

In comparing the general form of a man with that of a frog we must take into consideration the fact that man stands erect with the axis of his body at right angles to the ground while we think of the frog with the axis of its body more or less parallel to the ground. To make the parts correspond we must stand the frog up like a man. When we do this the anterior or front of the man corresponds to the ventral side of the frog while the posterior or back of the man corresponds to the dorsal side of the frog. In man the term **superior** corresponds to anterior in the frog and **inferior** to posterior.

The human body is divided into head, neck, thorax, and abdomen. The neck allows the head to be turned and moved about upon the shoulders. This is a great advantage to a land animal but would be a disadvantage to any animal which lives and, like the frog, swims under water. A fish has no neck nor has a whale. The trunk of the frog is not divided into thorax and abdomen. The division of the trunk of the mammal into thorax and abdomen is an adaptation to its method of breathing which will be described later.

In standing the frog up to compare him with a man we have put his nose in the air and made him open his mouth to the sky, which is an attitude only rarely assumed by man. While man carries his body erect his face is directed forward at right angles to the axis of his body so that his mouth, nose, eyes, and ears have approximately the same position with reference to the ground on which he stands as those of a dog or frog in the natural resting position. The human face is much shortened in comparison with that of a frog and the mouth is smaller. The eyes look directly forward, giving binocular vision, and lie deep in their orbits protected by the bones of the skull. The eardrum is hidden and lies at the end of a trumpet formed by the external ear and the auditory canal.

2. THE SKELETON OF THE FROG AND OF MAN

A. CARTILAGE AND BONE

Two kinds of material occur in the skeleton of vertebrates, cartilage and bone. Cartilage is what is commonly referred to as gristle. It consists of a stiff jellylike matrix formed by cells which remain irregularly scattered through it and continue to grow and divide (Fig. 4:12). In bone the matrix is made hard by a deposit of calcium carbonate and calcium phosphate; and the bone cells which are contained in small cavities or lacunae in the bone are arranged in concentric layers around the central marrow cavity or around the blood vessels contained in the bone (Fig. 4:12). Cartilage is enclosed in a membrane of living cells called the **perichondrium.** All bones are enclosed in a similar membrane called the **periosteum.** In the living body the bones are joined together or articulated to form joints, movable or immovable.

The vertebrate skeleton may be divided into an **axial skeleton** consisting of the **skull, vertebral column, ribs** (absent in the frog), and

sternum, and an **appendicular skeleton** consisting of the skeletal parts of the limbs and their supporting girdles (Fig. 27:2).

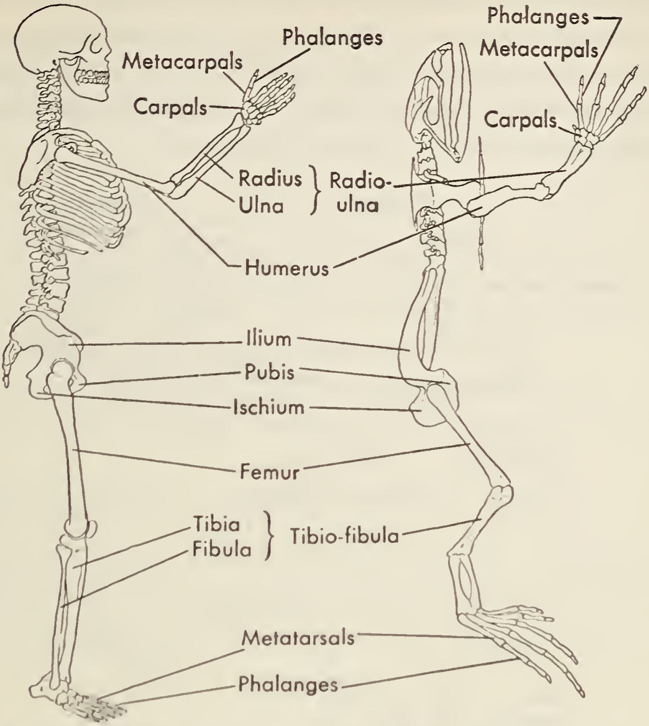
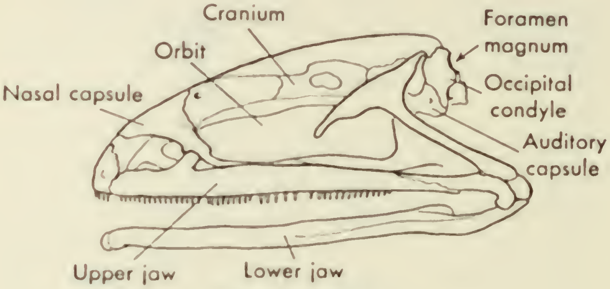


Fig. 27:2 The skeleton of a man and the skeleton of a frog.

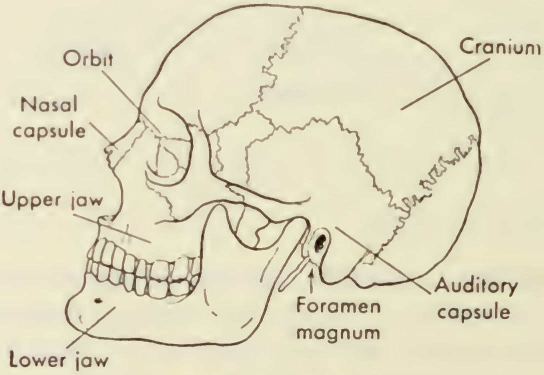
B. THE FROG'S SKULL

The **skull of the frog** consists of a number of bones and cartilages which are firmly joined together except at the angles of the mouth where the joints between the upper and lower jaws occur (Fig. 27:3). It is a flattened structure and, when looked at from above, triangular in shape. Indeed it seems at first sight to consist of little more than two jaws closing the enormous mouth. The **cranium** is a small, elongated box occupying the central dorsal portion. Between the cranium and the upper jaw and serving to attach the two together are the **capsules** for the organs of special sense, the nose, eye, and ear. The **nasal capsules** continue the cranium forward to the front of the upper jaw. They enclose the nasal cavities which open to the exterior by the **external nostrils** and into the mouth cavity by the **internal nostrils.** The **orbits** are rounded spaces on either side of the cranium in which the eyeballs are lodged. On each side posteriorly between the upper jaw and the cranium is an **auditory**

capsule in which is lodged the internal ear. A large posterior opening in the cranium called the **foramen magnum** (L. *foramen*, an opening, + *magnum*, large) puts the cranial cavity in communication with the neural canal of the vertebral column. Through the foramen magnum the spinal cord becomes continuous with the brain. Ventral to the foramen magnum is a pair of rounded projections, the **occipital condyles** by which the skull articulates with the vertebral column.



SKULL OF FROG



SKULL OF MAN

Fig. 27:3 Above, side view of frog skull; below, side view of human skull.

C. THE HUMAN SKULL

Compared with that of the frog the **human skull** is relatively much more compact (Fig. 27:3). The cranium forms a much larger portion, and the jaws a much less conspicuous part. The nasal capsules form the skeleton of the nose. The orbits are deep set and completely enclosed at the back and sides. The auditory capsules have become incorporated in the base of the cranium behind the articulations of the lower jawbones.

D. FUNCTIONS OF THE SKULL

A number of different functions are performed by the skull of which the chief are the following:

1. Protection of the brain. This is the most primitive and most important function of the skull and is carried out chiefly by the cranium.
2. To provide attachment and a skeleton for jaws, which make possible the seizing and (in many animals) the mastication of food. The most primitive fishes are without jaws, having sucking mouths.
3. Protection and support for the organs of special sense. This is the function of the nasal and auditory capsules and the orbits.
4. In fishes and certain of the more primitive amphibians the skull provides a skeletal support for the gills.
5. In air-breathing vertebrates the skull provides the rigid walls of a respiratory passage through which air is sucked into the lungs.

E. THE VERTEBRAL COLUMN OF THE FROG

The vertebral column of the frog consists of nine vertebrae plus a long rodlike bone called the **urostyle** which extends posteriorly. A **typical vertebra** (Fig. 27:4) consists of a ventral solid portion, oval in cross section, called the **centrum**, which supports a **neural arch**. The centrum and neural arch surround the **neural canal**. In the neural canal is lodged the spinal cord, a portion of the central nervous system. The neural arch and centrum together form a structure resembling a signet

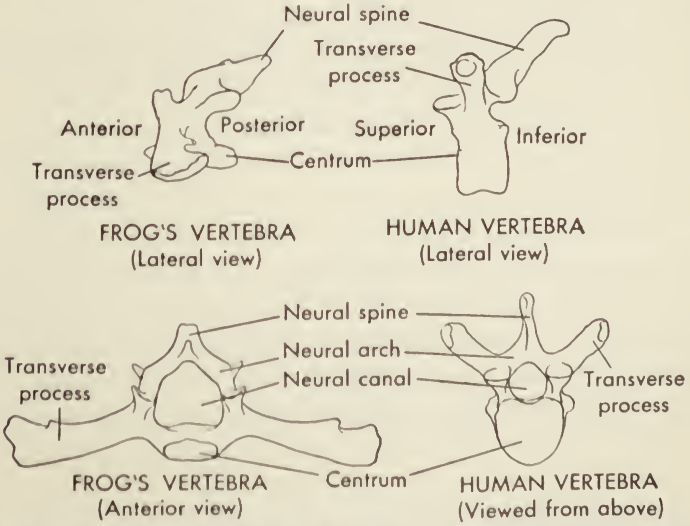


Fig. 27:4 Typical vertebrae of frog and man. Similar views for comparison.

ring, the centrum being the signet, and the spinal cord occupying the position which would be occupied by a finger. Extending dorsally from the neural arch is the **neural spine** and laterally on each side a **transverse process.** The centra of the vertebrae are joined together by a series of pads of cartilage to form the vertebral column or backbone. The first vertebra, called the **atlas,** is without transverse processes and has a pair of oval facets for articulation with the occipital condyles of the skull. In the ninth or **sacral vertebra** the transverse processes are enlarged for attachment of the pelvic girdle.

F. THE HUMAN VERTEBRAL COLUMN AND RIBS

The vertebral column of man shows the same general plan as that of the frog but is more complicated. The individual vertebrae (Fig. 27:4) differ in the different parts of the body so that five regions are recognized, as follows: cervical, thoracic, lumbar, sacral, and coccygeal or caudal. The **cervical vertebrae** are in the neck and support the head. It is an interesting fact that there are the same number of cervical vertebrae in man, namely seven, as in most of the higher mammals, including the giraffe. The first cervical is called the **atlas,** the second the **axis.** There are twelve **thoracic vertebrae** to which the twelve ribs are attached. Five **lumbar vertebrae** follow these, distinguished by their prominent transverse processes. In a child there are five **sacral vertebrae** to which the pelvic girdle is attached. In an adult these five vertebrae are fused together to form one solid bone, the **sacrum.** The **coccygeal vertebrae** consist of three or four small nodules of bone, man's vestige of a tail.

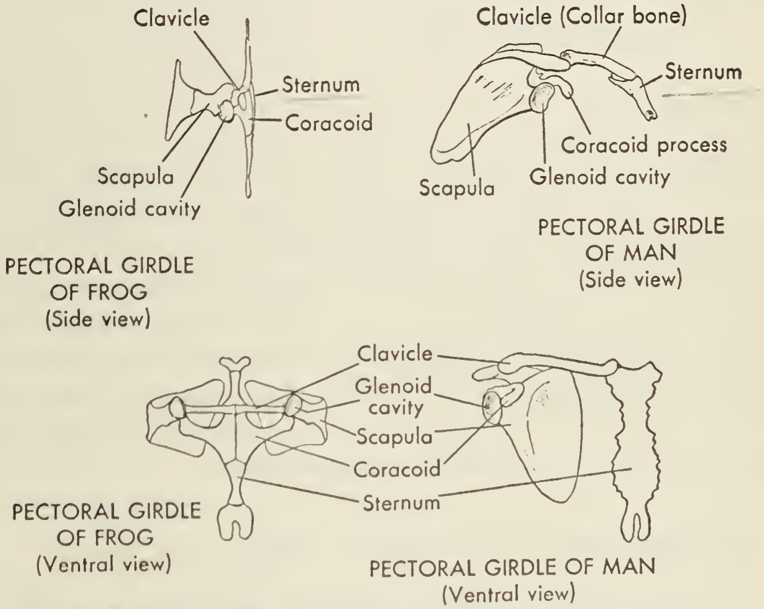
The **ribs** in the human skeleton are long, thin bones attached to the thoracic vertebrae at the back and curved like a boomerang. The first seven are also attached to the **sternum,** a flat bone in the front of the chest, and are called **true ribs.** Of the remaining five, called **false ribs,** three are attached by **costal cartilages** to the sternum and the other two, called **floating ribs,** are unattached in front. The functions of the ribs and sternum will be discussed later in connection with the respiratory system.

G. THE FUNCTIONS OF THE VERTEBRAL COLUMN

The vertebral column or backbone forms a more or less rigid rod extending the length of the trunk and tail (when present) and supported in front by the forelimbs and behind by the hind limbs. From this rod are hung the various soft parts of the body enclosed in the muscular body wall. This function of the backbone is very conspicuous in a horse or cow. In man and other vertebrates which assume the erect or semi-erect attitude this function is in part performed by the bones of the thorax and shoulders, which, however, are dependent upon the vertebral column for their support. The vertebral column also supports the skull and forms the skeleton of the tail, when one is present.

H. THE PECTORAL AND PELVIC GIRDLES OF THE FROG

The **pectoral girdle** serves for attachment of the fore limbs. In addition to supporting a portion of the weight of the body in most animals, the fore limbs also act as shock absorbers. It is thus an adaptation in the frog that the pectoral girdle to which the fore legs are attached is not joined directly to the vertebral column. Although the frog is without ribs it possesses a **sternum** in approximately the same relative position as in man (Fig. 27:5). This forms the ventral portion of the girdle. The lateral portions of the girdle each consist of four bones, extending around the sides of the body to the back where they remain quite separate from the vertebrae. Three of these bones form a tripod, two legs of which, formed by the **clavicle** and **coracoid**, are attached to the sternum. The third leg consisting of the **scapula** extends dorsally and has attached to it a **suprascapula**. The three legs of the tripod meet at the **glenoid**



PECTORAL GIRDLE OF FROG (Side view)

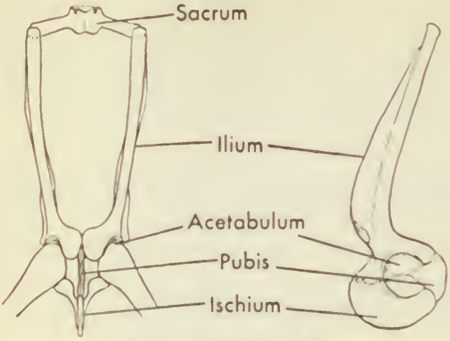
PECTORAL GIRDLE OF MAN (Side view)

PECTORAL GIRDLE OF FROG (Ventral view)

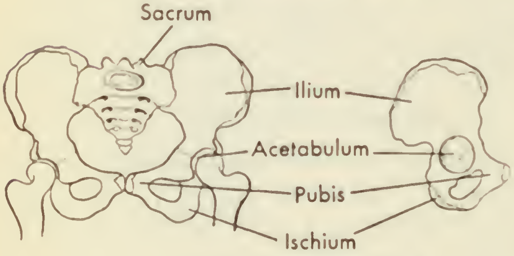
PECTORAL GIRDLE OF MAN (Ventral view)

Fig. 27:5 Pectoral girdles of frog and man. Similar views for comparison.

cavity into which the fore limb articulates. It is easily seen that such a tripod provides not only a good attachment for the limb but is also a good shock absorber.



PELVIC GIRDLE OF FROG



PELVIC GIRDLE OF MAN

Fig. 27:6 Pelvic girdles of frog and man. Similar views for comparison.

The **pelvic girdle** may also be regarded as consisting of two tripods (Fig. 27:6). However, the two ventral legs of the tripod, the **pubis** anterior and the **ischium** posterior, which correspond to the clavicle and coracoid of the pectoral girdle, are short and articulated together in the mid-line, there being no bone here .corresponding to the sternum. The dorsal leg of each tripod, the **ilium** which corresponds to the scapula, is long and articulates with the transverse process of the sacral vertebra. The cavity into which the hind leg articulates, and which is situated where the three parts of the tripod meet, is called the **acetabulum.**

I. THE PECTORAL AND PELVIC GIRDLES IN MAN

In the human pectoral girdle the clavicle, here called the collar bone, is attached to the upper part of the sternum but the coracoid is represented by a mere knob of bone, the **coracoid process** attached to the scapula or shoulder blade. On account of man's erect posture the pelvic girdle is a large and important part of his skeleton. On each side the three bones, ilium, pubis, and ischium, are fused to form a large **innominate bone,** which is attached at the back to the sacrum and in front to its mate at the **symphysis pubis.** The bony structure formed by the sacrum, the two innominate bones, and the coccyx is called the **pelvis.** The bony pelvis forms a thick irregular ring around a cavity, the **opening of the pelvis.** Through this opening the child passes at birth and the size of its head, if it is to be born naturally, is limited by the size of this opening in the mother.

The **functions** of the pectoral and pelvic girdles must be sufficiently apparent from the above discussion of their relation to the fore and hind limbs.

J. THE LIMBS IN THE HUMAN SKELETON

It will be more instructive to describe first the limbs of the human skeleton (Fig. 27:2). The bone of the upper arm is called the **humerus.** Its upper end or "head" fits into the glenoid cavity. The fore arm contains two bones, the **radius** and **ulna.** If the arm is held out to the side at right angles to the body so that the palm of the hand is to the front and the thumb turned up, the radius and ulna are parallel and the radius is uppermost. When the hand is rotated in this position so as to turn the palm backwards and the thumb down, the radius and ulna become crossed. There are eight small bones in the wrist called the **carpals,** arranged in two rows of four each. In the body of the hand are five **metacarpals,** each corresponding to a digit. In each finger there are three **phalanges,** and in the thumb two.

If the leg of a human skeleton be held out to the side in a position parallel to that in which the arm was held in the above description and with the big toe upward and the sole of the foot forward, the correspondence of the bones in the two appendages becomes evident. The thigh bone is called the **femur** and corresponds to the humerus. Like the fore arm the shank contains two bones, the thicker of these bones is called the **tibia** or shin bone. It corresponds to the radius, while the thinner bone, called the **fibula,** corresponds to the ulna. The ankle corresponds to the wrist; it contains seven irregularly shaped bones, the **tarsals,** of which the largest is the **heel bone.** The instep corresponds to the body of the hand and, like it, contains five bones, the **metatarsals.** The big toe, which corresponds to the thumb, has two **phalanges,** while each of the other toes has three.

K. THE LIMBS IN THE FROG'S SKELETON

Turning now to the frog (Fig. 27:2), we find in the fore limb the humerus, corresponding to the same bone in man. The radius and ulna are fused to form a single bone, the **radio-ulna,** but the line of fusion is clearly to be seen. In the wrist there are six carpals arranged in two rows, three in each. Beyond these are five metacarpals. The thumb is rudimentary and represented only by the small metacarpal; of the other digits the two outer have each three phalanges, while the two inner have two. In the hind limb the femur corresponds to the human bone of that name. As in the case of the fore limb the tibia and fibula are fused to form a **tibiofibula.** The ankle of the frog is elongated to give additional leverage for jumping. This elongation is produced by the interposition of two elongated and fused bones between the end of the tibiofibula and the tarsals proper, which latter are reduced in size and number. There are five well-developed metatarsal bones. The first digit which corresponds to the big toe in man has two phalanges, as has also the second toe. The third and fifth digits have three phalanges each and the fourth digit four.

The various functions which the pectoral and pelvic appendages have taken upon themselves in the different groups of vertebrates is an interesting story which, unfortunately, cannot be told here.

L. METAMERISM AND HOMOLOGY

In the vertebrate skeleton there are numerous indications of a primitive **metamerism** of the vertebrate body, a feature which carries us back to the invertebrates — to the earthworm and the crayfish. Metamerism is conspicuous in the vertebral column and the series of ribs. The vertebrae and ribs are, however, actually formed between the metameres. In comparing the skeleton of a frog with that of a man, part for part, we have been able to trace out the **homology** of the parts and in many cases it must have become obvious to the student that bones called by the same name in the two skeletons are homologous. Further, the arm and leg of man correspond in their structure and mode of attachment to the body, and in consideration of the metamerism indicated by the vertebral column occur in different segments. We therefore have here an example of **serial homology,** such as already seen in the series of appendages of an arthropod. In this connection it will be well for the student to refer to the discussion of homology in Chap. 24.

3. JOINTS

The different bones of the skeleton are joined together by immovable joints as in the skull, slightly movable joints, such as those between all of the vertebrae except the atlas and axis, and freely movable joints, such as those of the limbs. In all cases a softer substance is placed between the bones.

In the skull, with the exception of the lower jaw, the bones are locked together by interdigitating projections forming jagged lines of union, called **sutures.**

The centra of the vertebrae and the two pubic bones of the pelvis are held together by discs of fibrous cartilage, forming what is called a **symphysis.** Such a joint permits of a slight movement because of the elasticity of the cartilage.

A typical movable joint, such as one of those in the limbs, is enclosed in a ligamentous **capsule** composed of fibrous tissue (Fig. 27:7). The end of each bone is covered by a smooth layer of cartilage, the **articular cartilage.** Between the articular cartilages is a viscid lubricating fluid, the **synovial fluid,** secreted by the synovial membrane which lines the **joint cavity.** When the bones are moved at the joint the smooth surfaces of the articular cartilages slip past each other, lubricated by the synovial fluid. In some cases (Fig. 27:7) an articular disc is interposed between the two articular cartilages, separating the joint cavity into two cavities.

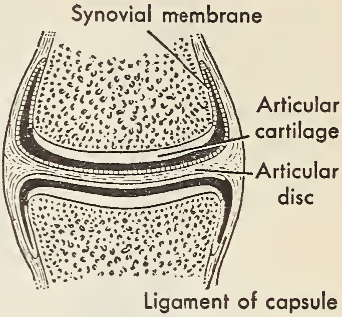


Fig. 27:7 Diagram of a section of a movable joint with an articular disc of cartilage. The synovial fluid is solid black. After Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, The Macmillan Company.

4. THE VOLUNTARY MUSCLES

The voluntary or skeletal muscles cover the skeleton and constitute a large part of the bulk and weight of the vertebrate body. They are referred to as voluntary because they are directly under the control of the will. In this respect they are different from the muscles of the intestines and other internal organs which are normally not under the control of the will and are, therefore, called involuntary. Voluntary muscles vary in shape according to the work which they perform. The muscles which form the abdominal wall are wide, thin sheets of tissue, while the muscles of the arms and legs are in many cases like long thick straps.

As an example of a typical muscle, we will choose the **gastrocnemius muscle** (Fig. 27:8), which forms the calf of the hind leg and is similar in all ambulatory vertebrates, including man. This muscle is attached at one end, called the **origin,** to the back or posterior surface of the lower or distal portion of the femur. At the other end, called the **insertion,** it is continued into a long tendon, the **tendon of Achilles,** which passes round the back of the heel and is attached to the heel bone. The origin of a muscle is defined as the part which remains relatively fixed with regard to the body when the muscle contracts. The insertion is the end or part which moves relatively to the rest of the body. The effect produced by the contraction of a muscle is called its **action.** The gastrocnemius muscle has a double action as its contraction may produce one or both of two effects; it may straighten out the foot, making the man or animal rise on its toes, or it may bend the leg at the knee back toward the thigh. The first of these is called extension and when functioning in this way the muscle is called an **extensor** of the foot, while the second is known as flexion and the muscle is said to be a **flexor** of the leg.

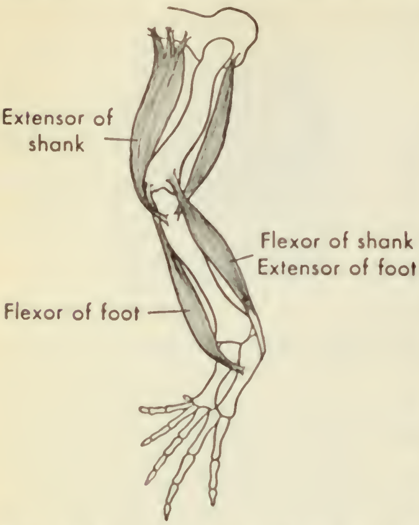


Fig. 27:8 Opposing muscles in the leg of a toad. The gastrocnemius muscle is labeled on the right. It is a flexor of the shank and an extensor of the foot. The peroneus muscle is a flexor of the foot. After Hegner, *College Zoology*, The Macmillan Company.

Seldom, if ever, does a muscle of the body come into action alone. Muscles occur in groups which act together and in harmony to produce certain movements. Each group of muscles is usually opposed by an **antagonistic** group which so to speak "takes up the slack" and gives precision and steadiness to the movement. Thus among the muscles in the frog which oppose the group to which the gastrocnemius belongs is the peroneus, situated in the front of the leg, arising on the front of the femur, and inserted on the upper surface of one of the heel bones. This muscle extends the leg and flexes the foot in the frog. In man these movements involve somewhat more complicated and specialized groups of muscles.

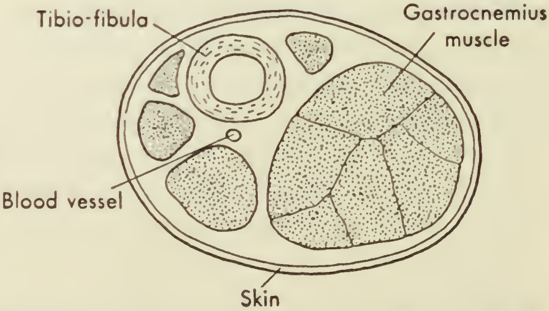


Fig. 27:9 Cross section of shank of frog's hind leg, showing gastrocnemius muscle and other structures. The clear areas between the muscles contain connective tissue.

A voluntary muscle is composed of many bundles of **muscle fibers,** bound together by connective tissue (Fig. 27:9). **Connective tissue,** which forms the binding and packing of the body, is, like all tissues, cellular, but it contains besides irregular cells many fine fibers produced by the cells and woven together to form a more or less loosely matted material in the meshes of which the connective tissue cells lie. The **muscle fibers** (Fig. 27:10) of voluntary muscles are exceedingly long, cylindrical bodies, which may reach in an adult a length of several inches, although only 0.01 millimeter (1/250 inch) in diameter. They contain numerous nuclei (Fig. 4:13).

Running lengthwise through the cytoplasm of the muscle fiber are numerous fine **fibrils.** The muscle fiber is surrounded by a membrane called the **sarcolemma.** It is believed that the contractility of the muscle fiber is due to the fibrils. Each fibril consists of a succession of light and dark portions, like dark and light beads on a necklace, and as the dark and light positions of the fibrils correspond across a muscle cell, the whole cell seems to be divided into short dark and light bands. Because of this, voluntary muscle is also called **striated muscle.** Striated muscle fibers should not be regarded as cells since each one contains numerous nuclei.

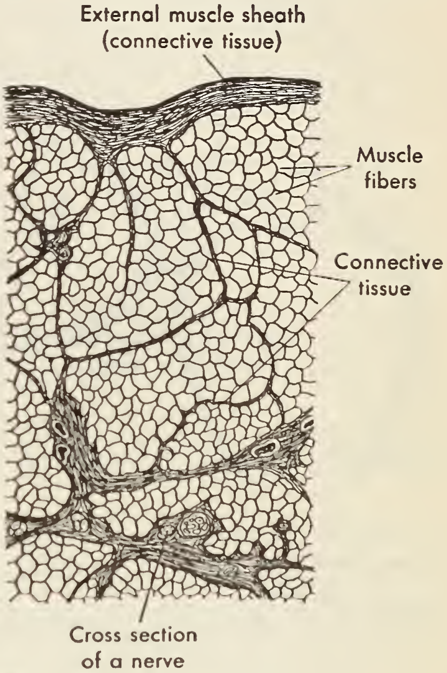


Fig. 27:10 Cross section of a human muscle. After Bremer, *A Textbook of Histology*, by permission of P. Blakiston's Son and Company.

Muscle fibers contract in response to a stimulus received through a nerve fiber. The nerve fibers make contact with the muscle fibers through special end organs called **motor end plates.** When a muscle contracts, usually not all of the muscle fibers in it contract. The force exerted by the muscle depends on the number of fibers contracting.

To do work muscles must be supplied with energy. This the muscle obtains by oxidizing the sugar glucose. This sugar and also the oxygen are brought to it in the blood vessels with which most muscles are plentifully supplied.

5. THE BODY CAVITY

The body wall of the frog surrounds and encloses the body cavity or **coelom.** This extends from just behind the mouth to the posterior end of the trunk, and contains various organs such as the stomach, intestine, and liver. The organs contained in the body cavity constitute the viscera. The body cavity is almost completely filled by the viscera which float in a small amount of clear liquid called the **coelomic fluid.** The coelomic fluid permits the movement of the viscera within the body cavity. As a result of the contractions of the involuntary muscles which they contain the separate organs in the body cavity are slowly but almost continuously changing their shape and position. The part of the coelom which contains the heart is separated from the rest of the body cavity by a membranous sac, the **pericardial sac.** The cavity of this sac, which surrounds the heart and contains coelomic fluid, is called the **pericardial cavity.** The remainder of the coelom which contains most of the viscera is called the **peritoneal** or **abdominal cavity.** Thus the coelom of the frog is divided into abdominal and pericardial cavities (Fig. 27:11).

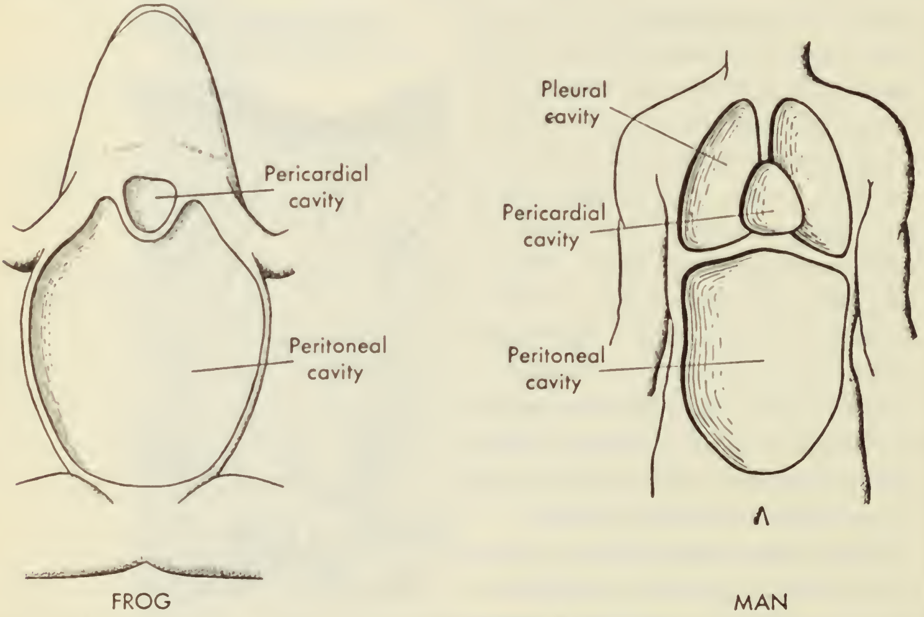


Fig. 27:11 Comparison of the body cavities of the frog and man.

The abdominal cavity is everywhere lined by a moist glistening membrane, the **peritoneum,** which secretes the coelomic fluid. The peritoneum envelops the viscera, covering them with a similar moist and glistening membrane. The viscera are loosely attached to the body wall by thin sheets of connective tissue containing blood vessels and nerves. These membranous sheets are covered on each side by peritoneum. When the organ is a part of the digestive tract the membranous sheet is called a **mesentery.** A transverse section of a frog in the abdominal region shows the distribution of the peritoneum (Fig. 27:12).

In **man and mammals** generally the coelom is still further divided by the **diaphragm,** a sheet of muscle and connective tissue extending transversely across the middle of the body. The diaphragm passes in man inferior to (in other mammals posterior to) the pericardial sac and separates two lateral cavities containing the lungs, and hence called **pleural cavities,** from the peritoneal cavity. Thus in man there are four divisions of the coelom, the pericardial cavity, two pleural cavities, and the peritoneal cavity. This does not include two cavities, the scrotal cavities, which occur in the male only and will be described in the chapter on reproduction. The relations of the peritoneum and mesenteries are similar in man and the frog.

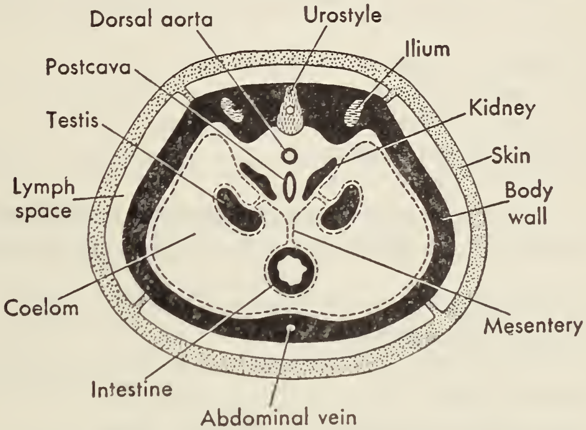


Fig. 27:12 Transverse section of a frog in the abdominal region. The peritoneum is indicated by a dotted line.

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Questions

1. Make a list of the adaptations which can be recognized in the external features of the frog.
2. What does man gain from the erect posture?
3. Distinguish between cartilage and bone.
4. Compare the skull of a frog with that of a man.
5. Discuss the functions of the skull.
6. Describe a typical vertebra.
7. Account for the differences between the pectoral and pelvic girdles in the frog. Do the same for the differences between the pectoral and pelvic girdles of man.
8. Discuss the serial homology of the human limbs.
9. Describe a typical freely movable joint.
10. Discuss the action of the gastrocnemius muscle of the frog or man.
11. Describe a muscle fiber.
12. Compare the coelomic cavities of the frog and man.

CHAPTER 28

The Digestive System

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1. A GENERAL ACCOUNT OF THE PROCESS OF DIGESTION

The function of the digestive system is to prepare the food materials for absorption by the cells of the wall of the small intestine. As must have become clear from the discussion of the plasma membrane, the number of organic substances which can pass through this membrane is relatively small and confined to a few types. It is therefore necessary that organic food materials should be transformed in order to be absorbed. In the vertebrate different parts of the alimentary tract have become specialized to perform different types of transformation. After its capture and while still in the mouth cavity the food material may be submitted to the first steps in the digestive process. Not all vertebrates chew their food, indeed the majority do not. In mammals the food is not only masticated in the mouth but it is also there submitted to the action of enzymes secreted by the salivary glands which attack the carbohydrates. After passing through the esophagus the food is churned in the stomach and acted on by enzymes produced by the wall of the stomach which affect chiefly proteins. The food is retained in the stomach by the pyloric valve until it reaches a creamy consistency, after which it passes into the small intestine. It is here, in the small intestine, that the most important digestive changes occur as a result of the action of enzymes from the pancreas and from glands in the intestinal wall. These enzymes acting on the proteins, fats, and carbohydrates reduce them to the simpler organic substances which can be absorbed. Absorption occurs chiefly through the walls of the small intestine. The function of the large intestine, into which the remaining material passes, seems to be chiefly the absorption of water. Before passing to a more detailed study of digestion it is desirable to go over the anatomy of the organs involved.

2. THE MOUTH CAVITY OF THE FROG

The frog feeds on insects and other small animals. It catches insects on the wing by flipping out its **tongue,** which is attached at the front of the mouth (Fig. 28:1). Worms and other crawling forms are caught between the jaws. The frog has teeth on its upper jaw, **maxillary teeth,** and on the roof of its mouth, **vomerine teeth.** The frog does not chew its food but swallows it whole, using its teeth only to seize it.

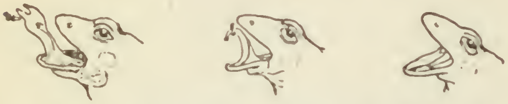


Fig. 28:1 Movements of tongue of frog. Redrawn after Hegner, *College Zoology*, The Macmillan Company.

The **mouth** (Fig. 28:2) is lined by a **mucous membrane** which is ciliated except on the tongue. Tubular mucous glands open into the front of the mouth and provide a sticky mucus with which the tongue becomes covered. Posteriorly the mouth is continuous with the gullet or esophagus.

Communicating with the mouth are various openings not directly concerned with digestion but best considered here. On the roof near the front of the upper jaw are the **internal** or **posterior nares.** The posterior nares connect with the external nares or nostrils through the **nasal cavities.** On either side of the **pharynx** near where the upper and lower jaws join at the angles of the mouth are the openings of the **Eustachian tubes.** The Eustachian tubes lead to the middle ears and will be considered later in the description of those organs. On the floor of the mouth in front of the opening of the esophagus and between the two backward projecting forks of the tongue is a longitudinal slitlike opening, the **glottis,** which leads through the larynx to the lungs. The portion of the mouth into which the glottis opens is known as the pharynx. When the frog swallows, the food has to pass the glottis in order to reach the esophagus; when this occurs the glottis is involuntarily closed by the two lips of the

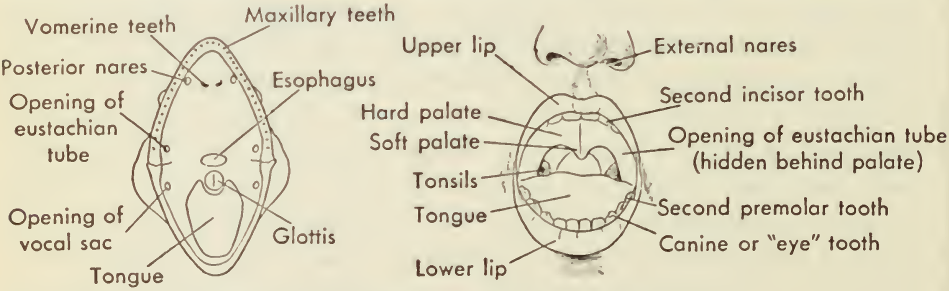


Fig. 28:2 Comparison of the mouth cavities of the frog and man.

slit coming together. This peculiar and at times rather unfortunate arrangement by which the food must cross the air passage occurs in all air-breathing vertebrates.

3. THE MOUTH AND NASAL CAVITIES OF MAN

In order to compare the relations of the organs in the head of the frog and man, one must imagine the frog's head bent at right angles to the rest of his body, the bend being made about the middle of the head. The mouth and nasal cavities then remain horizontal while the pharynx becomes vertical. The similarity in structure then becomes evident (Figs. 28:3 and 28:5).

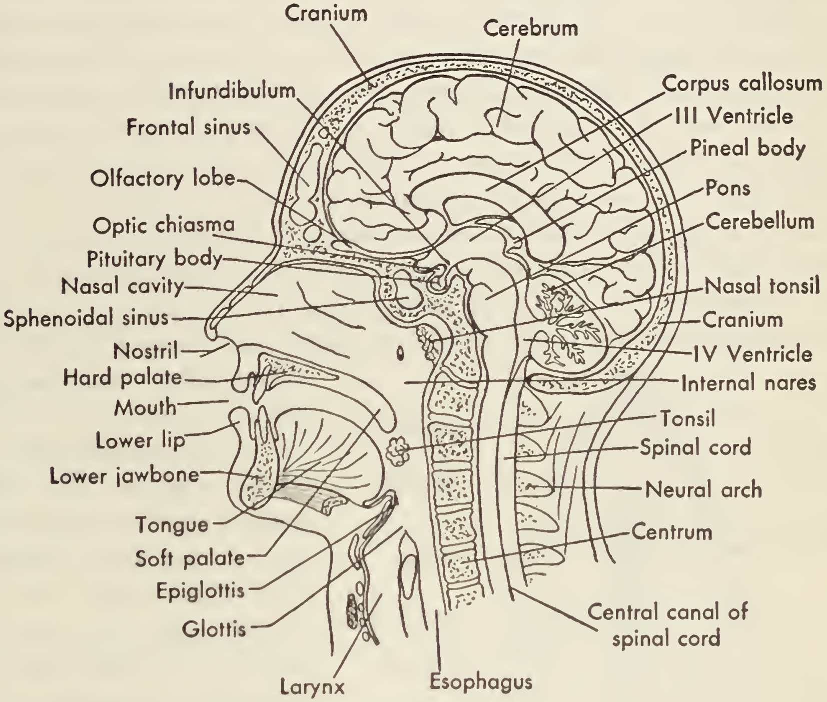
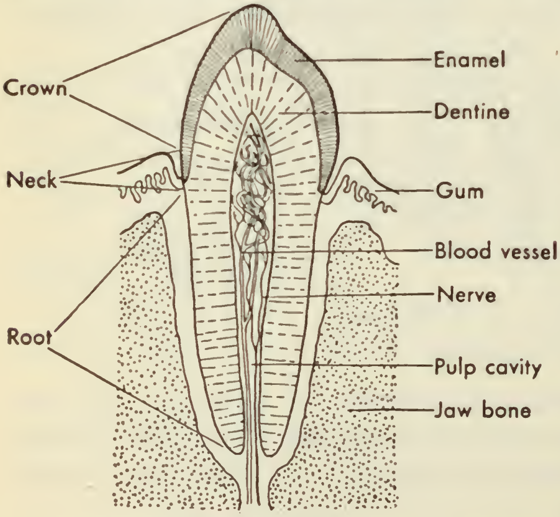


Fig. 28:3 Sagittal section of the human head.

The human **nostrils** or external nares correspond in position and function to the similarly named structures in the frog. The **nasal cavities** in man are relatively larger than those of the frog and the internal nares open at the back of the mouth instead of near the front as in the frog, being separated from the mouth cavity by a structure called the **palate.** Each of the nasal cavities contains three thin irregularly coiled sheets of bone, the turbinates, which are covered by a mucous membrane, the **olfactory membrane,** which contains cells sensitive to odors. The palate forms the roof of the mouth. The anterior portion, called the **hard palate,** contains a bony plate while the posterior portion, the **soft palate,** is muscular. The human pharynx is divided for the purposes of description into a **nasopharynx,** situated behind the nose, into which the **internal nares** open, and an **oral pharynx,** situated behind the mouth and tongue into which the glottis opens. The glottis and the opening of the esophagus into the mouth are in the same relative positions as in the frog, so that here also the food in order to reach the esophagus must pass the glottis. In man the glottis is closed during swallowing by a lidlike structure, the **epiglottis,** attached anteriorly at the root of the tongue.

We proceed to consider the human mouth in somewhat more detail. In this the student is advised to study his own mouth with the aid of a mirror (Fig. 28:2). The margins of the upper and lower jaws project into the cavity of the mouth and are covered with a rather firm tissue forming the **gums.** The **teeth** are fastened into sockets in the jaws. The normal number of permanent teeth in man is thirty-two, sixteen in each jaw. In front are the eight **incisors,** two on each side of each jaw, next come the **canines** or "eyeteeth," not large like those of the dog but nevertheless recognizable, then on each side of each jaw two **premolars** and three **molars.** The third molars are the wisdom teeth and do not always appear. The **milk teeth,** the first set of teeth, are twenty in number corresponding to all of the permanent teeth, excepting the twelve molars which appear only in the permanent set.



CANINE TOOTH

Fig. 28:4 Longitudinal section of a tooth. The cement which unites the dentine of the root with the bone of the jaw is not shown. It occupies the clear space surrounding the root.

A typical tooth consists of a **root, neck,** and **crown** (Fig. 28:4). The crown is the part above the gum and is covered with **enamel.** The neck is the portion surrounded by the gum. The root is the portion imbedded in the jawbone. It is covered by a bony layer called **cement,** and firmly united with the jawbone by connective tissue. The body of the tooth is composed of **dentine** or **ivory,** a substance which is similar to bone.

The roots of all the teeth except the molars are single. The upper molars have three roots and the lower molars two roots. Each tooth contains a central **pulp cavity** extending down to the tip of the root or roots. Into this cavity go blood vessels and nerves. A tooth dies or is killed when the blood vessels and nerves in the pulp cavity are destroyed.

The incisor and canine teeth have chisellike crowns and are used for biting and tearing the food. The premolar and molar teeth have flattened crowns and are used for grinding and crushing the food. In the dog and cat the incisors are small and of little use, the canines are large and the chief offensive organ of the dog, while the premolars have sharp edges more adapted for tearing flesh than for grinding food, the dog and cat being naturally carnivorous or flesh-eating animals.

In man the soft palate hangs down at the back of the mouth. Behind and below it on either side are the **tonsils,** reddish masses of tissue. The openings of the **Eustachian tubes** lie above the palate and behind the nose. Communicating with the nasal cavities are a number of **air sinuses.** In front, directly above the nose, is the **frontal sinus,** at the back of the nasal cavities is the **sphenoidal sinus,** and on either side in the bone of the upper jaw is a **maxillary sinus.** Infection of these air spaces is the cause of "sinus trouble." Failure of the epiglottis to close when swallowing causes the food to "go the wrong way." In swallowing the soft palate moves upward and shuts off the nasal cavities from the mouth, a circumstance which makes it possible for some people to drink a glass of water while standing on their heads.

4. THE DIGESTIVE SYSTEM OF THE FROG

We will now consider the digestive tract and associated digestive glands of the frog, leaving the discussion of the process of digestion and the functions of the different parts until after the human digestive system has been considered.

The gullet or **esophagus** leads directly from the back of the mouth to the stomach. There is no distinct boundary between the esophagus and stomach, the transition from the one to the other being gradual. The esophagus of frogs is remarkably distensible. Bullfrogs have been known to swallow sparrows. The **stomach** bulges out on the left side (Fig. 28:5) and gradually tapers to end in the **pyloric constriction,** a valvular structure by which the passageway from the stomach to the intestine can be opened or closed by the relaxation or contraction of circular sphincter muscles. Small tubular glands in the lining of the stomach secrete the gastric juice.

The **intestine,** which constitutes the remainder of the alimentary tract, is, in the frog, divided into three regions called the **duodenum, ileum,** and **rectum,** and terminates in the **cloaca.** The duodenum and ileum together form the **small intestine,** while the much larger rectum constitutes the **large intestine,** although by some authors the cloaca also is included in the large intestine. The duodenum is relatively short and of small diameter. It is distinguished from the rest of the digestive tube by having opening into it the ducts of the liver and pancreas. The ileum has approximately the same diameter as the duodenum but is much longer and closely coiled. The **rectum** is a thin-walled saclike structure almost equal in length and diameter to the stomach. It leads into the cloaca. The cloaca (Latin for "sewer") is short and thick walled; into it the ducts of the excretory and reproductive organs open. The opening of the cloaca to the exterior at the extreme posterior end of the frog is called the **anus.** The cloaca is a structure not found in the higher mammals and man, the rectum of these animals opening directly on the surface of the body. The stomach, small intestine, and rectum are attached to the dorsal body wall along the line of the vertebral column by a **mesentery,** as already stated in the section on the body cavity. In this mesentery run the blood vessels and nerves to the various parts of the alimentary tract.

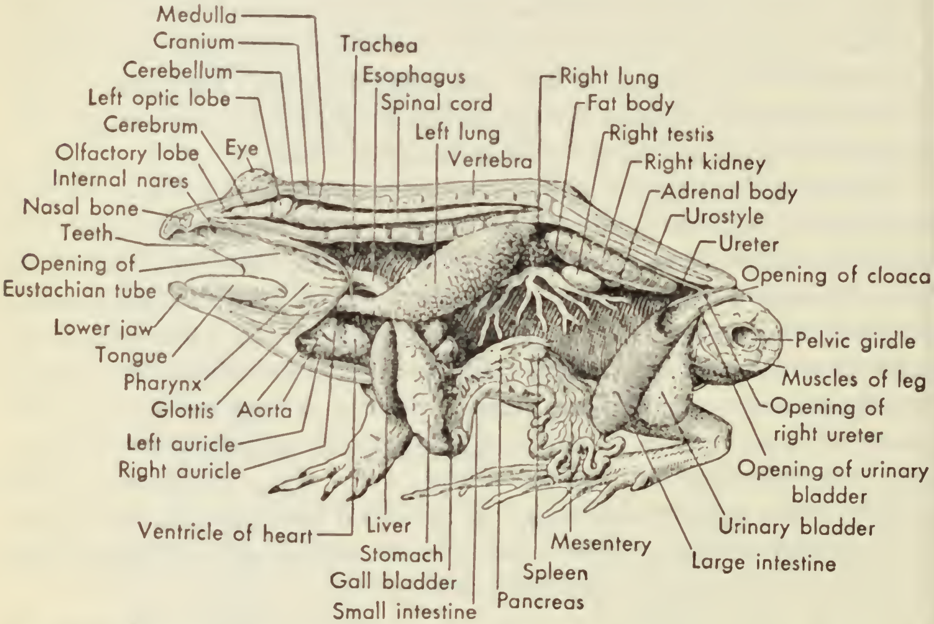


Fig. 28:5 Diagram of a lateral dissection of the internal organs of a frog. From L. L. Woodruff, *Foundations of Biology*, The Macmillan Company.

The walls of the different portions of the digestive tube are similar in structure. The general plan of this structure is well shown in a **cross section of the small intestine** (Fig. 28:6). On the outside is a thin layer of **peritoneum** continuous with that of the mesentery. Within this is a layer of **longitudinal muscle** fibers which are cut across in the section and appear as small round bodies. Next comes a much thicker layer of **circular muscle fibers,** which since they run round the intestine are cut lengthwise and show as elongated cells. The next layer is the **submucosa,** a more or less spongy mass of connective tissue, containing lymph spaces. Lastly we come to the **mucosa,** the layer lining the cavity of the intestine. The mucosa consists of a single layer of columnar epithelial cells, elongated in a direction at right angles to the surface. There are two kinds of these cells, one kind called **goblet cells,** because they contain a large oval vacuole and secrete mucus; the other kind, called **absorptive cells,** are concerned with the absorption of the digested food, which process occurs mainly in the small intestine. The mucosa is relatively inelastic so that when the circular muscle fibers contract it is thrown into longitudinal folds, which appear in sections as projections into the cavity of the intestine. The movements of the intestine which are produced by the contractions of the longitudinal and circular muscle fibers will be discussed in connection with the human digestive system.

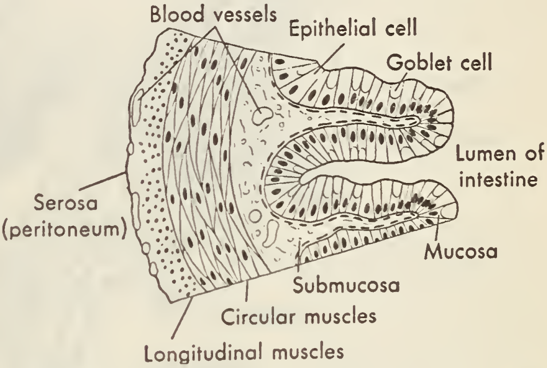


Fig. 28:6 Part of a cross section of a frog's intestine. Redrawn after S. J. Holmes, *Biology of the Frog*, The Macmillan Company.

The **liver** is the largest gland in the frog's body, and fills up a considerable portion of the anterior part of the body cavity (Fig. 28:7). Its secretion is called the **bile** or gall. Associated with the liver is a sac called the **gall bladder** in which the bile is stored. The bile leaves the liver in **hepatic ducts** and may be carried from these ducts either directly to the duodenum through the **common bile duct,** or may pass first to the gall bladder to be stored there and later carried through the common bile duct. This is made possible by the way in which the hepatic ducts from the right side of the liver join with the **cystic ducts** from the gall bladder to form the common bile duct which also receives the hepatic ducts from the left side. Bile may thus pass either from the liver to the gall bladder, from the liver directly to the duodenum, or from the gall bladder to the duodenum. The common bile duct passes through the pancreas on its way to the duodenum.

The **pancreas** is a flattened, irregularly lobed gland located in the membrane extending between the liver and the duodenum, called the **duodeno-hepatic ligament.** The **pancreatic duct** opens into the common bile duct as the latter passes through the pancreas. There is no pancreatic bladder, the pancreatic juice being secreted as required by a mechanism described later in this chapter.

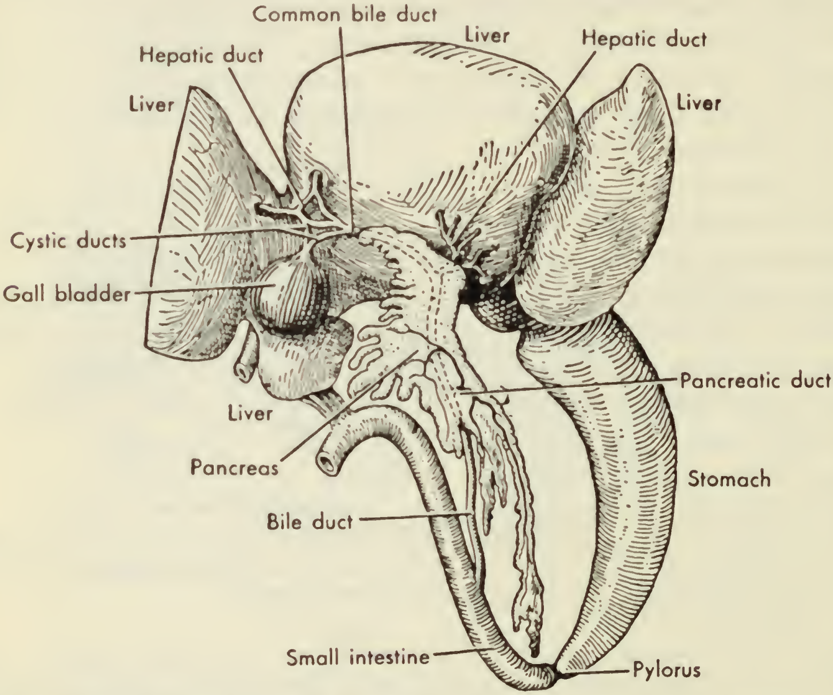


Fig. 28:7 Frog. Ventral view of a dissection of the liver, gall bladder, pancreas, and their ducts. Lobes of the liver are turned forward. From L. L. Woodruff, *Animal Biology,* The Macmillan Company.

5. THE DIGESTIVE SYSTEM OF MAN

Three pairs of **salivary glands** supply the saliva: the **submaxillary glands,** one on the inner side of each of the lower jaws, the **sublingual glands** below the tongue, and the **parotid glands** on the side of the upper jaw just in front of the ear (Fig. 28:8). The **ducts** of the first two of these glands open on the floor of the mouth in front of the tongue, the ducts of the parotid glands open on the inner sides of the cheeks. The cells of the salivary glands take certain substances from the blood and from them manufacture, in their protoplasm, the secretion which they pass out into the duct.

In man the **esophagus** is a long, almost straight, tube extending through the neck and thorax to the abdomen which it enters by piercing the diaphragm. During its course through the neck and thorax it runs just in front of and parallel to the vertebral column. Normally, when food is not being swallowed, it is collapsed and lies, like a flat tire, between the vertebral column behind and the windpipe or trachea in front.

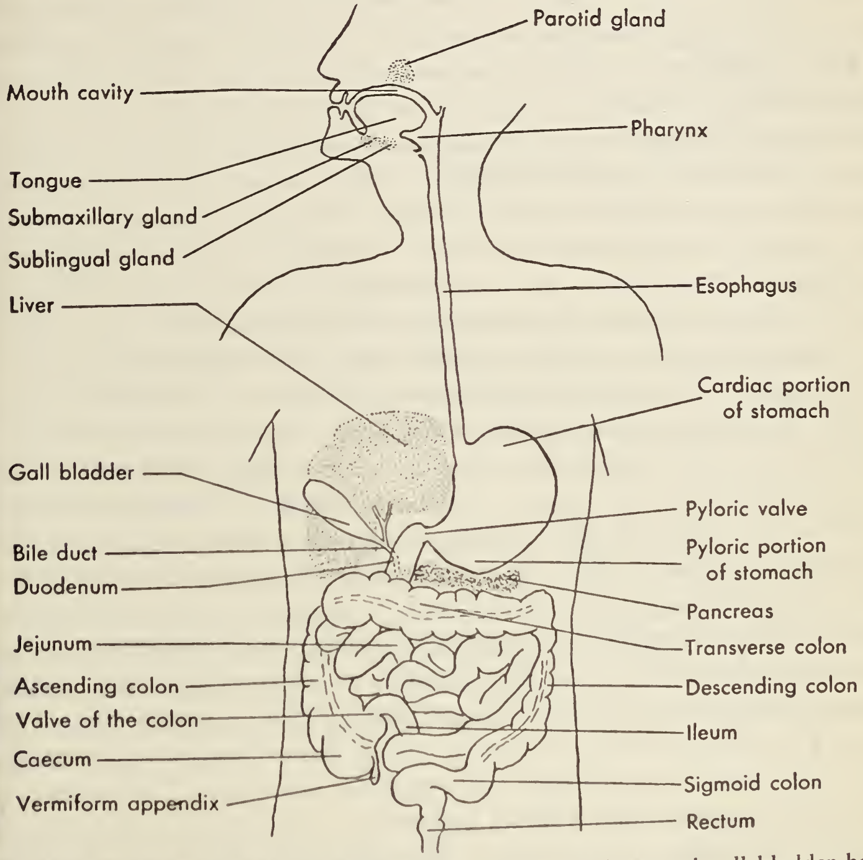


Fig. 28:8 Diagram of the human digestive system. The liver and gall bladder have been turned upward and to the subject's right, and the stomach has been raised.

The **stomach** is a large pear-shaped sac bent somewhat in the form of a "J" which lies just under the diaphragm on the left side of the peritoneal cavity. The inner portion of the J is known as the **lesser curvature**, the outer portion as the **greater curvature**. However, the shape and position of the stomach vary according to the amount of food it contains. Although often somewhat larger in people with a "potbelly," it is usually only partly responsible for the front extension which is more often due to the deposition of fat under the skin and in the part of the mesentery known as the great omentum or apron. The esophagus opens into the stomach on one side, the side nearest the center of the body. This part of the stomach, which is near the heart, is called the **cardiac portion.** The lower part leading to the pyloric constriction is called the **pyloric portion.**

The **duodenum** in man is not essentially different from that in the frog. It differs somewhat in its position in the peritoneal cavity, being fixed against the posterior abdominal wall, an adaptation to man's erect posture. As in the frog the duodenum receives the common opening of the bile and pancreatic ducts, which join just before the opening is reached. The rest of the small intestine is rather arbitrarily divided into **jejunum** and **ileum.** These latter parts are connected to the dorsal abdominal wall by a large fan-shaped mesentery which helps to retain them in place and through which pass large arteries and veins supplying this part of the intestine. The small intestine has a total length of about 20 feet.

The ileum opens into the side of the large intestine so that there is a blind portion of the latter about 2½ inches in length. This blind portion at the beginning of the large intestine is called the **caecum.** In some herbivorous mammals the caecum reaches an enormous development, exceeding in volume, when filled, the whole of the rest of the digestive tube. It is quite large in the rabbit. Attached to the caecum is the notorious wormlike **vermiform appendix,** seat of appendicitis. The opening of the ileum into the caecum is guarded by a valve called the **valve of the colon** which prevents material from passing back into the ileum. The ileum joins the caecum in the lower part of the peritoneal cavity on the right side and it is there that the appendix is located. The portion of the large intestine which follows, beginning at the entrance of the ileum, is called the **colon** or large bowel. The colon is a large, relatively thin-walled tube, ranging in diameter from about 2½ inches where it leaves the caecum to roughly 1½ inches where it joins the rectum. Its length is about 5 feet. Three ribbonlike longitudinal bands run the length of the colon and seem to take tucks in it, so that the tube itself is sacculated. The colon forms an almost complete circle in the abdominal cavity, and is divided into the ascending, transverse, and descending colons. The **ascending colon** extends upward on the right side, the **transverse colon** crosses the body in front of the stomach just below the liver, while the **descending colon** passes down the left side to join the rectum in the cavity of the pelvis. In its course the colon makes several sharp turns or flexures, including the S-shaped, **sigmoid flexure** where the descending colon passes into the pelvic cavity. The **rectum** is a relatively but not actually straight tube about 6 inches in length leading from the colon to open on the surface of the body at the anus. The anal aperture is guarded by a **sphincter muscle** which is attached anteriorly and posteriorly. The contraction of this muscle, which is under control of the will, contracts the aperture into a narrow slit.

The **liver** lies just under the diaphragm, mainly on the right side. On this side the lower front margin reaches slightly beyond the lowest rib. It is a large compact mass, weighing about 3 pounds. The **gall bladder** is a green sac shaped like a much elongated pear. Where the stalk of the pear would be the gall bladder becomes continuous with a duct, the **cystic duct,** which carries the bile to and from it. Into the cystic duct open **hepatic ducts,** bringing the bile from the liver to the gall bladder except when food is being digested, when the bile from both the liver and gall bladder passes down the **common bile duct** to the duodenum.

The **pancreas** is an elongated irregular gland which lies against the posterior abdominal wall near the duodenum, into which its duct opens by the same opening as the bile duct. The pancreas is much smaller than the liver, weighing usually about 3 ounces. In man, as in the frog, the pancreas has no bladder.

As in the case of the frog the portion of the digestive tract in the abdominal cavity is attached to the body wall by mesenteries. Through these mesenteries branches of the main blood vessels and nerves pass to and from the digestive organs. Where the mesentery is attached to the greater curvature of the stomach it is extended to form a large thin-walled sac, the **great omentum,** which in life hangs down in front of the abdominal organs.

Topical Outline of Chapter 28

1. A general account of the process of digestion 543
2. The mouth cavity of the frog 544
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4. The digestive system of the frog 547
5. The digestive system of man 550

Questions

1. Describe the mouth cavity of the frog.
2. Compare the mouth and nose of a man with the corresponding structures in a frog.

3. Make a diagram of the permanent teeth in man and show which are represented in the milk teeth.
4. Describe the structure of a tooth.
5. Where are the salivary glands located in man?
6. Where are the sinuses? What do they contain? Where do they open?
7. Compare the digestive tract of the frog with that of man.
8. Make a diagram of a cross section of a frog's intestine.

Suggestions for Further Reading

Holmes, Samuel J., *The Biology of the Frog*, The Macmillan Company, New York, 1928, Chaps. IV and VII.

Kimber, D. C., C. E. Gray, and C. E. Stackpole, *Textbook of Anatomy and Physiology*, The Macmillan Company, New York, 1935, Chaps. XVII, XIX, and XX.

CHAPTER 29

Food Materials and Metabolism

1. FOOD SUBSTANCES

The food of man consists of the bodies of plants and other animals, i.e., of protoplasm, for it is mostly the protoplasmic part of the animal or plant rather than the cell products, such as the cell walls of plants or the cartilage and bones of animals, which is utilized. Cooking has chiefly the effect of destroying the cell walls of plants and the connective tissue of animal flesh and thus making the protoplasm more accessible to the digestive juices.

The chemical composition of protoplasm has already been considered at some length in Chaps. 5 and 6. There we found among the inorganic constituents water and various inorganic salts, which were present in the form of ions, and among the organic substances carbohydrates, fats, and proteins. Water and a number of inorganic salts are essential constituents of a diet. The inorganic salts do not need to be digested; being soluble they can be absorbed directly. Most foods contain some or all of the different kinds of inorganic and organic materials, but in different proportions. An idea of the composition of some common foods can be obtained from Table 29:1.

TABLE 29:1. COMPOSITION OF SOME COMMON FOODS

	PER CENT				
FOOD	WATER	PROTEIN	FAT	DIGESTIBLE CARBOHYDRATES	INORGANIC MATERIAL
Meat	76.7	20.8	1.5	0.3	1.3
Eggs	73.7	12.6	12.1		1.1
Cow's milk	87.7	3.4	3.2	4.8	0.7
Wheat bread	35.6	7.1	0.2	55.5	1.1
Potatoes	75.5	2.0	0.2	20.6	1.0
Fruit	84.0	0.5		10.0	0.5

Carbohydrates and fats are used by the body almost exclusively as sources of energy. Proteins are essential to repair broken-down tissue and to build new tissue but they may also be used as sources of energy. A person can exist on an entirely meat diet, as does the Eskimo, because it contains all the essential materials, but he will starve to death on a diet containing only fats and carbohydrates.

Only in a few cases are organic food materials absorbed through the intestinal wall in their original form. Carbohydrates must be changed to monosaccharides if not already such; fats must be changed to fatty acids and glycerine; and proteins must be broken up into amino acids. It thus comes about that only a few different organic substances are actually used. How these are obtained is largely a matter of convenience, taste, and the ability of the digestive enzymes to break up the materials in which they occur. Each cell of the body forms its own kinds of proteins and each protein has a different amino acid content. There are no special brain foods, muscle foods, etc., although each of these organs may require different proportions of the basic food substances.

2. ACCESSORY FOOD SUBSTANCES

Although carbohydrates, fats, and proteins provide the energy and most of the building materials needed by the body, they alone are not sufficient to maintain the body in normal health. Certain other substances are required although in relatively small amounts. These are called **accessory food substances** and include a number of minerals and the vitamins.

A. MINERALS REQUIRED BY THE BODY

The minerals required by the body are usually obtained either with the food materials in the diet or dissolved in the drinking water. The need of the body for any chemical element and the effect of deficiency in this element can be determined experimentally by feeding animals diets deficient or entirely lacking in the element in question. From such experiments the data given in the table have been accumulated (Table 29:2).

B. VITAMINS

It has been found that a diet which contains all of the food substances mentioned in the previous sections is insufficient, at least in many of the higher animals, to produce normal growth and health. Certain sub-

TABLE 29:2. SOME OF THE MORE COMMON MINERALS REQUIRED BY THE BODY *

ELEMENT	FOR WHAT REQUIRED	EFFECT OF DEFICIENCY
Calcium	Bones, teeth, blood, nerves, muscles, milk production, heart	Poor development of bones, rickets, dental deficiency, excessive bleeding, excessive nervous irritability
Phosphorus	Bones, teeth, muscles, blood, metabolism of carbohydrates and fats, activation of enzymes	Poor development of bones and teeth, rickets, retarded growth
Magnesium	Bones, nerves, muscles, heart, ion balance, enzymes	Retarded growth, nervousness Rapid or irregular heart beat
Potassium	Normal growth, muscle function, ion balance, osmotic pressure	Nerve disorders, irregular heart beat, poor muscular control
Chlorine	Regulation of osmotic pressure, activation of enzymes, gastric juice	Loss of body weight, loss of water. Digestive disturbances
Sodium	Regulation of osmotic pressure	Loss of body weight, nerve disorders
Iodine	Thyroxine (secretion of thyroid gland). Regulation of basal metabolism	Low basal metabolism, nervous disturbances, overweight
Iron	Hemoglobin	Decreased hemoglobin
Sulphur	Body proteins	Retarded growth

* Silicon and fluorine have recently been shown to be required.

stances known as vitamins are essential although required in only very small quantities. A **vitamin** is an organic compound which is required for the normal growth and health of an animal but only in very small amounts. Vitamins do not furnish the energy for chemical reactions nor do they furnish building material for the cell. With the exception of vitamin D, and then only as regards the final stages, animals are in general unable to synthesize vitamins in their own bodies and are dependent upon plants for them.

A vitamin is identified by the effect which its absence from the diet produces. Most vitamins are manufactured by plants and come to animals in the plants which they eat. Some vitamins can be formed in the animal body. Since vitamins are effective in exceedingly small quantities — for some of them the daily dose for a healthy adult is measured in fractions of a milligram — their extraction in pure form has been attended with considerable difficulty. Later studies have frequently shown that what was considered to be a single substance is in reality two or more separate vitamins. This has led to much confusion in the nomenclature.

TABLE 29:3. VITAMINS

NAME AND CHEMICAL FORMULA	SOURCES	EFFECTS OF DEFICIENCY
Vitamin A Antikeratinizing Antiophthalmic Fat soluble $C_{20}H_{30}O$	Cod- and halibut-liver oils, vegetables, butter, eggs	Susceptibility to infections of the epithelial tissues of eyes, respiratory system, alimentary canal, digestive glands, kidneys; night blindness
Vitamin B_1 Antineuritic Thiamin $C_{12}H_{17}ON_4SClHCl$ (Now manufactured synthetically)	Yeast, cereals, vegetables, fruits, cheese, kidney, liver, milk	Beriberi (nervous disease) with loss of appetite, loss of weight and vigor, subnormal temperature
Vitamin B_2 Vitamin G Riboflavin $C_{17}H_{20}N_4O_6$	Liver, egg white, leafy vegetables, yeast, fruits, milk	Scaly, greasy skin, dark inflammation of the tongue, itching and burning of eyes
Vitamin B_6 Pyridoxin $C_8H_{11}O_3N$ (Now manufactured synthetically)	Yeast, rice polishings, wheat, maize, especially the germs. Liver of mammals	Dermatitis in rats and chicks. Effects in man are little known but the vitamin is assumed to be necessary
Nicotinic acid Niacin $C_6H_5O_2N$ (Now manufactured synthetically)	Liver, adrenal gland, yeast, wheat	Pellagra characterized by lesions of the mucous membranes, e.g., mouth, nose; disturbances of gastrointestinal tract. Mental disorders
Pantotheric acid $C_9H_{17}O_5N$ (Now manufactured synthetically)	Liver and kidney, rice bran, molasses	Causes symptoms similar to pellagra in chicks. Human effect unknown, necessity not proved
Vitamin C Antiscorbutic Ascorbic acid Cevitamic acid $C_6H_8O_6$ (Now manufactured synthetically)	Orange and lemon juice, vegetables, fruits	Scurvy (disease which affects mucous membranes, joints, and bones), decay of teeth, loss of weight, fatigue
Vitamin D Provitamins D (ergosterol, $C_{28}H_{50}O$) Vitamin D (calciferol, $C_{28}H_{44}O$)	Cod-liver oil, butter, food irradiated with ultraviolet light	Rickets, a bone disease of children in which bones become soft and muscles weak, due to low content of calcium and phosphorus. Defects of teeth
Vitamin E Tocopherols Antisterility $C_{29}H_{50}O_2$, $C_{28}H_{48}O_2$	Wheat germ oil, lettuce, alfalfa	Failure to reproduce in rats. Affects both male and female. Germ cells fail to develop. Human effects not conclusively proved

TABLE 29:3. VITAMINS (*Continued*)

NAME AND CHEMICAL FORMULA	SOURCES	EFFECTS OF DEFICIENCY
Vitamin H Biotin $C_{10}H_{16}O_3N_2S$	Widely distributed vegetables, grains, nuts, liver, kidney, eggs	Skin and mucous membranes dry up. Appears to be required by most animals, including man
Vitamin K Antihemorrhagic Prothrombin factor $C_{31}H_{46}O_2$, $C_{41}H_{56}O_2$	Alfalfa, spinach, cabbage	Blood-clotting time prolonged due to reduced prothrombin content of blood. Required by animals, including man

VITAMIN A. Vitamin A is essential for the maintenance of the epithelial tissues of the body, especially those of the eyes, respiratory system, alimentary canal, digestive glands, and kidney. In its absence the skin becomes scaly, the intestine is less able to absorb, the conjunctiva and cornea of the eye become opaque. It has recently been established that vitamin A is essential for the formation of visual purple, its absence causing night blindness, a condition in which the person sees poorly at night.

Vitamin A is formed in the animal body from a yellow substance called **carotene** which is especially abundant in the roots of carrots. Carotene is also found in butter, egg yolk, fish-liver oils, and many fruit juices. When absorbed by the cells of the intestine carotene is transformed into vitamin A.

The next five vitamins to be discussed, viz., vitamin B_1, vitamin B_2, vitamin B_6, nicotinic acid, and pantotheric acid, together with a few less well-known vitamins, are sometimes grouped together as the "B complex" vitamins.

VITAMIN B_1. Vitamin B_1 is essential for the proper functioning of the nervous system. Its deficiency gives rise to a disease called **beriberi,** a nervous disease characterized by extreme weakness and neuritic pains. The chemical name of vitamin B_1 is **thiamin.** It is manufactured synthetically and sold under various trade names. It occurs abundantly in yeast and seeds. In seeds the vitamin is in the embryo — a part which is usually removed from wheat and rice grains when they are polished — hence the wisdom of using whole wheat and unpolished rice. Vitamin B_1 is intimately concerned with carbohydrate metabolism and plays a role in the oxidation of carbohydrates in tissues.

VITAMIN B_2, called also **riboflavin,** is apparently essential for all animals. Its fundamental action seems to be to take part in certain enzyme systems which regulate oxidation in cells. It is related chemically to one of these enzymes, the yellow or flavin enzyme. Riboflavin also takes part in carbohydrate metabolism. This vitamin can be synthesized more economically and more satisfactorily than it can be prepared from natural sources.

VITAMIN B_6, called also **pyrodoxin,** has not been proved necessary for human beings. Its effects have been studied chiefly on rats where its deficiency causes definite symptoms. It is believed to be concerned with the metabolism of fats and amino acids. The plant source must be cooked to ensure complete utilization of the vitamin B_6 by rats.

NICOTINIC ACID, called also **niacin,** is the antipellagra vitamin. Deficiency of this vitamin causes the condition known as pellagra, characterized by inflammation of the skin and mucous membranes, disturbances in the gastrointestinal tract, and mental disorders. Usually pellagra is due to deficiency in a number of vitamins and the condition can be corrected only by the administration of several or all of the vitamins of the B complex. Nicotinic acid appears to function mainly as a part of enzyme systems which take part in protein and carbohydrate metabolism by transporting hydrogen.

PANTOTHERIC ACID deficiency causes symptoms similar to pellagra in chicks. Its effect on human beings is unknown but it is thought that it is probably required by all living matter.

VITAMIN C. Absence of this vitamin from a diet causes scurvy, a disease familiar to sailors in the days of sailing ships when for long periods at sea they had no fresh food. Scurvy affects particularly the mucous membranes, causing them to swell and bleed. The vitamin occurs in oranges and other citrous fruits and certain vegetables.

VITAMIN D[1] occurs only in animals although plants contain the materials, called **provitamins,** from which the vitamin is formed. The best known of the provitamins is called **ergosterol.** When ergosterol is exposed to ultraviolet light, as occurs in the human skin when in the sun, the ergosterol is changed to calciferol which is a form of vitamin D.

VITAMIN E[2] has been called the reproductive vitamin because it appears to be necessary for reproduction although this has not been proved specifically for man.

VITAMIN H, called also **biotin,** occurs in all higher animals and in plants. Its physiological action is not clearly understood.

VITAMIN K is necessary for the maintenance of the capacity of the blood to coagulate. It is believed that vitamin K stimulates the production of prothrombin, a substance necessary for coagulation. It appears that normally this vitamin is formed by bacterial action in the intestines. It is absorbed only in the presence of bile.

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[1] Some five different "vitamins D" have been distinguished, but this phase of the subject will not be elaborated on here.

[2] Three different "vitamins E" have been distinguished corresponding to the three different forms of tocopherol.

Of considerable interest regarding some vitamins is their chemical relation to enzymes, e.g., riboflavin (vitamin B_2) to the yellow respiratory enzyme and others to hormones, e.g., calciferol (vitamin D) to the sex hormones.

3. DIGESTION

CHANGES UNDERGONE BY THE FOOD IN THE MOUTH. Since the frog swallows its prey whole and has no true salivary glands its food undergoes no change until it reaches the stomach. In man, however, important steps in the process of digestion take place in the mouth. In **mastication** the teeth cut and grind the solid materials, mixing them with the saliva into a more or less pasty mass. Besides large quantities of water, mucus, which acts as a lubricant, and certain salts, which render its reaction alkaline, the **saliva** contains two enzymes, **ptyalin** and **maltase,** which act to change the large molecules of starch into the simple molecules of the sugars, maltose and glucose. This involves the taking up of water. The starch molecule has been given the general formula $(C_6H_{10}O_5)_n$, where n is a large number. By the action of ptyalin and the addition of water it is changed to maltose, which has the molecular formula $C_{12}H_{22}O_{11}$. Some of the maltose may then change to glucose by the action of the enzyme maltase and the further addition of water. It will be noticed that the process of digestion of the starch molecule involves successive additions of water molecules to it. The chemical term for this is **hydrolysis.** Hydrolysis is characteristic of the digestion of many kinds of food substances. The enzymes of the saliva are active only in an **alkaline medium** such as the saliva usually is.

In the act of **swallowing** the food is collected together in a mass, called a **bolus,** on the upper surface of the tongue and pressed backward into the pharynx, the walls of which then relax and contract forcing it into the esophagus. During the passage of food into the esophagus the epiglottis is folded down closing the glottis, and the soft palate is moved upward closing the internal nares. The passage of the food down the esophagus to the stomach is involuntary and due to **peristalsis.** Peristalsis may occur anywhere along the length of the digestive tube. In peristalsis the circular muscle fibers of a short section of the tube, which are ordinarily in a state of partial (tonic) contraction, relax, forming a ringlike bulge into which the food materials pass. The relaxation lasts only for a short time and is followed by a contraction beginning at the upper portion of the bulge, i.e., the portion nearest the mouth. As this contraction develops, the portion of the tube immediately below begins to relax and the food materials are forced on into it. Thus rings of contraction pass down the tube, preceded by rings of relaxation, and force the contents gradually toward the anus.

CHANGES UNDERGONE BY THE FOOD IN THE STOMACH. After a meal, in a frog or a man the food collects in the stomach. The **gastric juice** contains about 0.5 per cent hydrochloric acid. The presence of this acid in the stomach tends to stop the action of the saliva. However, as the food is swallowed, it becomes arranged so that the part eaten last occupies the central portion of the bolus. As the gastric juice is secreted in the wall of the stomach it acts upon the peripheral portion first and penetrates only gradually into the mass of food, so that the salivary enzymes are able to continue their activity for a time. The gastric glands in the wall of the stomach are stimulated to secrete the gastric juice by nerve impulses which have their origin in the brain and result from the sensations of eating, and by chemical substances contained in the food. The gastric juice contains two enzymes, pepsin and rennin. **Pepsin** digests proteins to peptones in an acid medium. Peptones are stages in the hydrolysis of proteins. They are not absorbed in the stomach but require further digestion in the small intestine. **Rennin** acts on the soluble protein of milk and makes it clot to form a curd, as in "curds and whey." The curd must be further digested either by pepsin or in the small intestine. As digestion proceeds in the stomach the food mass becomes converted into a liquid called **chyme.** There is little or no absorption of digested food in the stomach. The chyme is passed gradually through the pyloric valve to the small intestine.

CHANGES UNDERGONE BY THE FOOD IN THE SMALL INTESTINE. The pancreas is stimulated to secrete the **pancreatic juice** by a substance called **secretin.** Secretin originates in the mucous membrane of the duodenum as a substance called **prosecretin.** The acid chyme when it enters the duodenum changes the prosecretin to secretin, which latter is absorbed through the walls of the intestine into the blood stream and carried to the pancreas where it exercises its stimulating effect. Secretin belongs to a class of substances called **hormones,** which are formed in one part of the body and carried in the blood stream to another part of the body which they stimulate to activity.

The **pancreatic juice** contains three powerful enzymes: trypsin, amylopsin or pancreatic diastase, and steapsin or pancreatic lipase. It has an alkaline reaction. **Trypsin** like pepsin produces hydrolysis of proteins, but it is able to carry the hydrolysis further and reduce them to their constituent amino acids. The pancreatic **diastase,** like ptyalin, produces the first stages of the hydrolysis of starch, forming maltose. The pancreatic **lipase** with the aid of the emulsifying action of the bile produces the hydrolysis of fats to fatty acids and glycerin.

The **bile** is secreted continuously by the liver and stored in the gall bladder. The mechanism by which it is released into the duodenum is somewhat similar to the mechanism by which the pancreatic juice is released from the pancreas. When fats or acids are in the intestine a hormone called **cholecystokinin** (Gr. *chole*, bile + *cystis*, bladder + *kinein*, to move) is passed from cells in the intestinal wall into the blood. The hormone is carried in the blood stream and reaches the gall bladder, the smooth muscles of which it stimulates, causing the expulsion of the bile. The bile is a thick, greenish, alkaline fluid, containing water, inorganic salts, and a number of organic substances, including bile salts and waste pigments which result from the absorption of broken-down red blood corpuscles by the liver, but no enzymes. Its digestive action, which is due to the bile salts, seems to be to emulsify fats, i.e., break them up into exceedingly fine droplets, and to activate the fat-digesting enzyme of the pancreas, lipase.

An important digestive juice is secreted by cells in the wall of the small intestine. It is called the **intestinal juice** and contains an enzyme called **erepsin** which hydrolyzes peptones to amino acids and thus continues the work of pepsin and trypsin. It also contains enzymes acting on carbohydrates including maltase which completes the work of the pancreatic diastase.

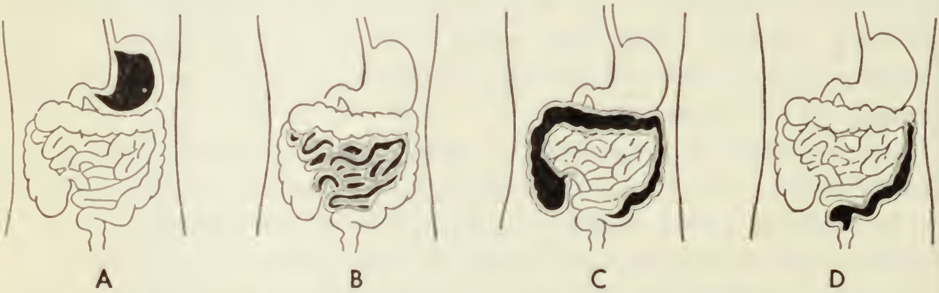
TABLE 29:4. ENZYME ACTIVITIES IN DIGESTIVE TRACT

WHERE PRODUCED	ENZYME	SUBSTANCE ACTED ON	RESULT OF ACTION	SUBSTANCES ABSORBED
Salivary glands	Ptyalin Maltase	Starch Maltose	Maltose Glucose	Glucose
Mucosa of stomach	Pepsin Rennin	Proteins Proteins of milk	Peptones Coagulation	
Pancreas	Trypsin	Proteins	Peptones Amino acids	Amino acids
	Diastase	Starch	Maltose	
	Lipase	Fats	Fatty acids Glycerin	Fatty acids Glycerin
Intestine	Erepsin	Peptones	Amino acids	Amino acids
	Maltase	Maltose	Glucose	Glucose
	Sucrase	Cane sugar	Monosaccharides	Monosaccharides
	Lactase	Milk sugar	Monosaccharides	Monosaccharides

CHANGES UNDERGONE BY THE FOOD IN THE LARGE INTESTINE. The walls of the large intestine secrete mucus but no enzymes. What digestion occurs in the large intestine is due to the continued activity of the enzymes which pass into it from the small intestine with unabsorbed material. The large intestine always contains large numbers of bacteria which cause the fermentation of food materials which may have, until now, escaped digestion. The material passed out in the feces consists of undigested parts of the food, large numbers of bacteria and the products of their activity, bile, and enzymes.

4. THE RATE OF MOVEMENT OF MATERIALS THROUGH THE ALIMENTARY CANAL

The passage of materials through the alimentary canal can be observed when the subject is given a "meal" containing a barium salt and X-ray pictures are taken at intervals (Fig. 29:1). Barium being one of the heavier elements is relatively opaque to X rays and casts a black shadow. Food after it is swallowed passes rapidly through the esophagus to the stomach (Fig. 29:1 A). There it may remain for 3 or more hours, depending on the meal. At the end of this time most of the meal passes gradually into the small intestine (Fig. 29:1 B). Twelve hours after the meal was swallowed, the undigested portion is practically all in the large intestine (Fig. 29:1 C). Here a considerable proportion of the water is absorbed and thirty-two hours after the meal was taken a considerable part of the undigested portion may be in the sigmoid colon ready for evacua-



A Immediately after swallowing meal. The barium is in the stomach.

B Four hours after intake of meal. The barium is in the small intestine.

C Twelve hours after intake of meal. The barium is in the colon.

D Thirty-two hours after intake of meal. The barium is in the descending and sigmoid colon.

Fig. 29:1 Diagrams showing the progress of a barium "meal" through the digestive tract as indicated by X-ray photographs taken at intervals. Barium is opaque to X rays and appears black in the X-ray shadow photographs. After a meal the upper or cardiac portion of the stomach usually contains some gas indicated here by the clear area.

tion through the rectum (Fig. 29:1 D). In the above account the times given are those of an average individual. Actually the time spent by the food materials in the different parts of the digestive tract varies greatly from individual to individual.

5. ABSORPTION

While the materials taken in the diet may be various the end products of digestion are practically always the same substances, although in varied amounts. All carbohydrates are reduced to simple sugars, most abundant of which is glucose. All fats are reduced to glycerin and fatty acids, there being but three common fatty acids. To be absorbed proteins must be split into their constituent amino acids, there being about twenty common amino acids. The materials absorbed through the walls of the alimentary tube consist, therefore, largely of water, inorganic salts, glucose, glycerin, fatty acids, amino acids, and vitamins.

Absorption takes place mainly in the small intestine, the absorbing surface of which is greatly increased by the presence of numerous microscopic fingerlike projections called **villi** (Fig. 29:2). Each villus is covered with a layer of epithelial cells and contains a network of capillaries surrounding a central lymphatic vessel called a **lacteal**. Glucose and amino acids pass through the epithelial cells and into the capillaries to be carried in the blood stream. Fatty acids and glycerin after being absorbed are resynthesized into fats by the epithelial cells of the villi and pass into the lacteals; with the lymph the fats are eventually carried into the blood stream. Water is absorbed chiefly in the large intestine.

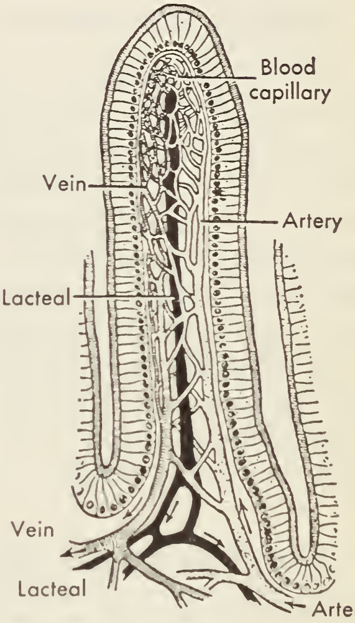


Fig. 29:2 Diagram of a section through a villus. Very highly magnified. The lacteal is shown in solid black. After Peabody and Hunt from L. L. Woodruff, *Foundations of Biology*, The Macmillan Company.

6. DISTRIBUTION OF NUTRIENT MATERIALS IN THE BODY

In the blood stream the absorbed substances are distributed to the different parts of the body. The veins which carry the blood from the intestine go first to the liver. There much of the sugar is taken out of the blood and stored as **glycogen** or animal starch, for the liver is the great storehouse of carbohydrates in the body. Some of the sugar, however, passes on to be taken up by the muscles, where it may also be stored as glycogen, or to other parts of the body. The fats are stored in different parts of the body in the cells of adipose tissue or what is commonly called "fat." The amino acids become generally distributed in the body and are used to build new proteins.

7. GENERAL METABOLISM

The term **metabolism** is applied in a general sense to all the chemical and energy changes which occur in the body. In a more restricted sense it is applied to particular substances, especially food substances, and refers to all the chemical and physical changes which these substances or their products undergo while in the body. Two phases of metabolism are distinguished: anabolism, the building up of materials, and katabolism, their breakdown. During growth anabolism exceeds katabolism. After growth has ceased and during normal adult life the two phases balance and there is equilibrium. In many diseases and in old age katabolism predominates. Anabolism requires energy. This energy and all of the energy required to carry on the various vital processes and activities of the body is supplied by katabolism.

A. CARBOHYDRATE METABOLISM

Carbohydrates such as starch and the disaccharides must be split up into monosaccharides, the most important of which is glucose, before they can be absorbed through the wall of the intestine. The monosaccharides are absorbed directly into the capillaries of the intestine. A special series of veins, comprising the hepatic portal system, carries the blood from the capillaries of the intestine to capillaries in the liver (Fig. 29:3). In the liver all of the sugar, except the small amount which is normally present in the blood, about 0.15 per cent, passes into the liver cells and is there transformed into **glycogen,** a carbohydrate similar to starch and having the same chemical formula. The glycogen is stored in the liver and changed back into sugar when it is needed to maintain the normal sugar content of the blood. Glycogen is formed and stored in this way also in the muscles. In other tissues sugar may be taken from the blood and synthesized into fats to be stored for future use in this form. The oxidation of sugar in the cells of the body is one of the main sources of energy for their vital activities. When oxidized in the tissues sugar forms carbon dioxide and water. The carbon dioxide is eliminated chiefly through the lungs, while water is passed out of the body in the form of urine, perspiration, and the moisture in the breath.

Carbohydrate metabolism is closely linked to muscular activity although carbohydrates do not take part in the actual mechanism of contraction. A resting muscle contains **phosphocreatine,** a compound containing phosphoric acid and creatine, the latter being an organic compound related in structure to glycine. The contraction of the muscle appears to be caused by the breakdown of the phosphocreatine into sodium phosphate and creatine. No oxygen is required for this reaction but it nevertheless provides the energy for the contraction. Another reaction, or rather series of reactions, follows rapidly and restores the muscle to its resting condition. Glycogen breaks down and forms lactic acid, $C_3H_6O_3$. Part of the lactic acid is oxidized to carbon dioxide and water. The energy yielded by this later reaction serves to convert the remainder of the lactic acid back to glycogen and to resynthesize phosphocreatine. The glycogen used up, i.e., that represented by the portion of the lactic acid which is oxidized, is replaced by glycogen formed from sugar taken from the blood.

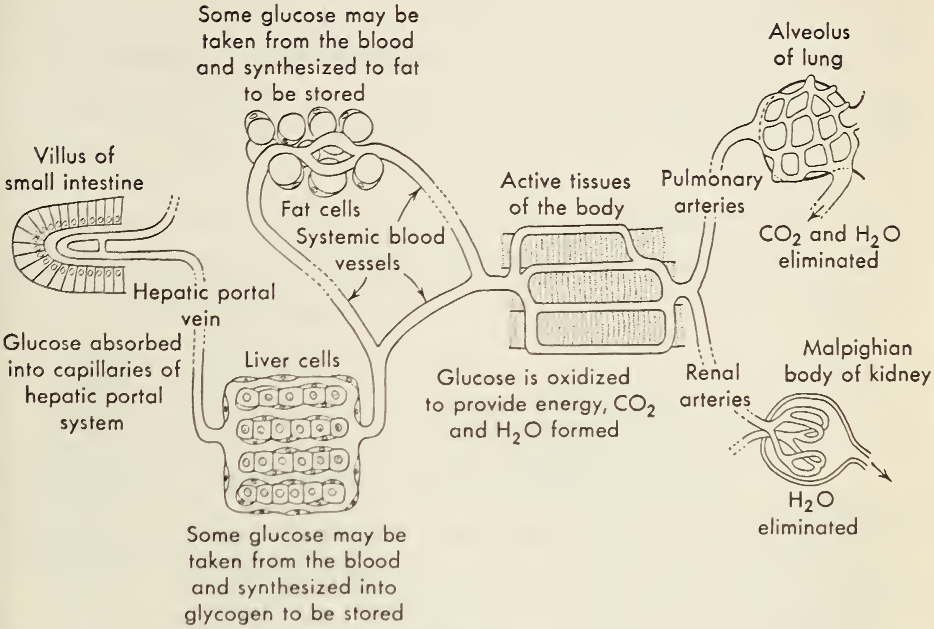

Some glucose may be taken from the blood and synthesized to fat to be stored
Alveolus of lung
Villus of small intestine
Active tissues of the body
Pulmonary arteries
Fat cells
Systemic blood vessels
CO_2 and H_2O eliminated
Hepatic portal vein
Glucose absorbed into capillaries of hepatic portal system
Liver cells
Malpighian body of kidney
Glucose is oxidized to provide energy, CO_2 and H_2O formed
Renal arteries
H_2O eliminated
Some glucose may be taken from the blood and synthesized into glycogen to be stored

Fig. 29:3 Diagram showing carbohydrate metabolism. Active tissue is indicated by striated muscle but glandular, nervous, or any growing tissue would serve equally well.

The transformation of glycogen in the muscle and the liver and the consequent release of chemical energy is controlled by a hormone called **insulin,** secreted by certain cells in the pancreas and carried in the blood. The cells which secrete insulin are grouped in little masses called the **islands of Langerhans** in the pancreas. The pancreas thus has two functions, that of secreting the pancreatic juice which passes to the intestine by the pancreatic duct, and the internal secretion of the hormone insulin into the blood. In certain forms of diabetes the cells in the pancreas which secrete insulin become diseased and fail to produce sufficient insulin with the result that the body is less able to utilize and store sugar. The excess sugar then appears in the blood and the urine.

B. FAT METABOLISM

Fats, after digestion into fatty acids and glycerol, are absorbed by the epithelial cells of the intestine and are there synthesized into fats which pass into **lacteals** in the villi. The digestion and resynthesis are necessary because the plasma membrane is impermeable to most fats as such and because each animal requires its own kind of fat. From the lacteals the fats pass in the lymphatic system to the thoracic duct and from it into the arterial blood stream. In the fatty tissues the fats pass out of the blood stream into fat cells where they form globules of fat. When needed to provide energy, the fats are first hydrolyzed into glycerol and fatty acids. The fatty acids are then oxidized, forming carbon dioxide and

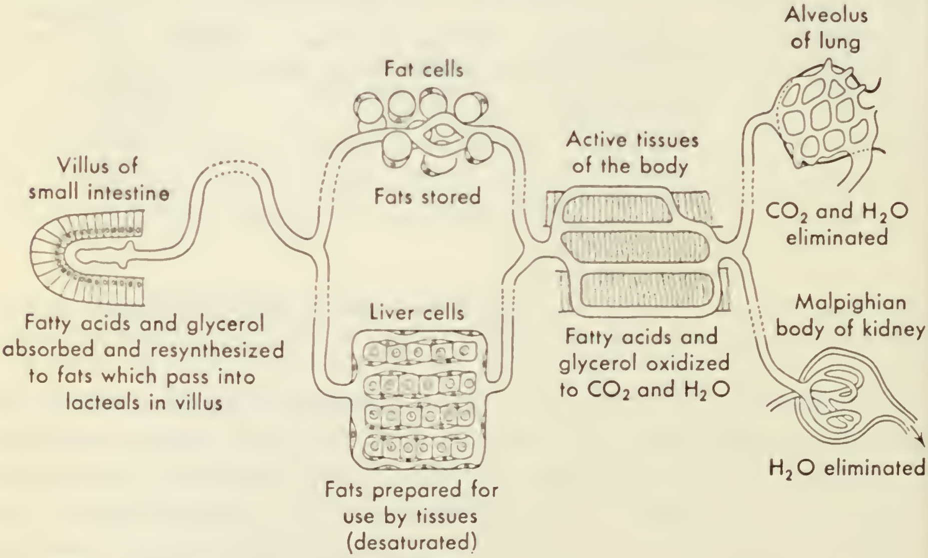

Alveolus of lung
Fat cells
Active tissues of the body
Villus of small intestine
Fats stored
CO_2 and H_2O eliminated
Liver cells
Malpighian body of kidney
Fatty acids and glycerol absorbed and resynthesized to fats which pass into lacteals in villus
Fatty acids and glycerol oxidized to CO_2 and H_2O
H_2O eliminated
Fats prepared for use by tissues (desaturated)

Fig. 29:4 Diagram showing fat metabolism.

water, which are eliminated in the same way as the waste products of carbohydrate metabolism (Fig. 29:4).

Besides being a source of energy, the fat in the body performs two other functions. On account of its being a poor conductor of heat, when spread in a layer under the skin, as it often is, it helps to keep the body warm. In certain parts of the body it forms cushions to protect organs or parts of the body as seen in the case of the soles of the feet and in the eye socket.

C. PROTEIN METABOLISM

Proteins are absorbed as amino acids. The **amino acids** serve two functions in the body. In the first of these they may be recombined to form proteins to replace proteins which have been broken down or to provide proteins required for the growth of cells. This is the anabolic phase. It seems a very roundabout method for the body to have to digest proteins into amino acids and then for the latter to be recombined again into proteins in the body. The explanation is to be found in the nature of the plasma membrane and the protoplasm of the cell. The plasma membrane is impermeable to nearly all proteins. When discussing the chemical composition of protoplasm it was stated that each species of organism has its own specific proteins different from those of other organisms and that these proteins are formed by different combinations of some twenty different kinds of amino acids. Thus one animal cannot

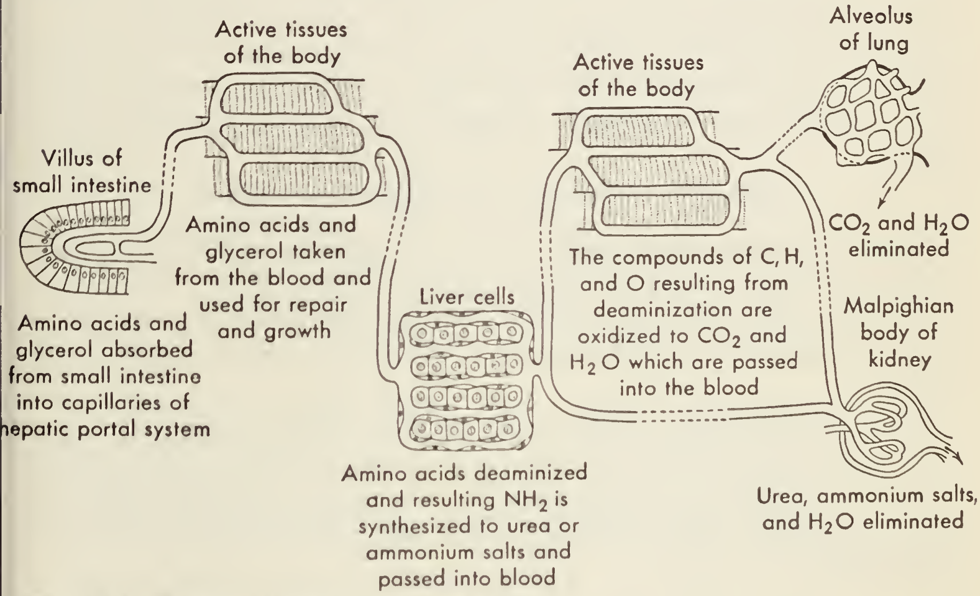

Active tissues of the body
Villus of small intestine
Amino acids and glycerol taken from the blood and used for repair and growth
Amino acids and glycerol absorbed from small intestine into capillaries of hepatic portal system
Liver cells
Amino acids deaminized and resulting NH_2 is synthesized to urea or ammonium salts and passed into blood
Active tissues of the body
The compounds of C, H, and O resulting from deaminization are oxidized to CO_2 and H_2O which are passed into the blood
Alveolus of lung
CO_2 and H_2O eliminated
Malpighian body of kidney
Urea, ammonium salts, and H_2O eliminated

Fig. 29:5 Diagram showing protein metabolism.

use directly the proteins of another animal or plant, but must first break them up into their amino acids and then select from these the kind and quantities required to build its own proteins.

When proteins are broken down in the tissues they yield amino acids (Fig. 29:5). Also not all of the amino acids absorbed into the blood are built up into proteins. These amino acids, e.g., those which result from protein katabolism and those which are not used for protein synthesis, are decomposed. This decomposition is outlined under proteins in Chap. 6. It includes **deaminization** (see Chap. 6), in which the amino acid molecule is split into ammonia and a simpler organic acid, and **decarboxylization,** in which the carboxyl group is split and a molecule of carbon dioxide is formed. The remainder of the molecule may now become oxidized to carbon dioxide and water, yielding energy.

The ammonia formed by the deaminization of the amino acids is a highly toxic substance. It is excreted from the body, mainly in the form of **urea,** $(NH_2)_2CO$, which is comparatively harmless. It is believed that the following series of reactions occur in the formation of urea from ammonia: the ammonia unites with water to form ammonium hydroxide, NH_4OH; this reacts with carbonic acid to form ammonium carbonate:

$$2NH_4OH + H_2CO_3 \longrightarrow (NH_4)_2CO_3 + 2H_2O$$

The ammonium carbonate $(NH_4)_2CO_3$ then loses two molecules of water to become urea. Urea is formed in the liver. This is shown by the facts that when amino acids are circulated through the liver the urea content of the blood increases and that when the liver is removed urea is not formed.

Most of the **nitrogen** which enters the animal body enters it as amino acid and leaves it as urea. The energy made available results chiefly from the oxidation of the amino acids. One gram of protein when digested, absorbed, and oxidized in the body yields approximately 4.1 kilocalories.

8. ENERGY CHANGES IN THE BODY

The frog is described as **cold blooded.** This does not really mean that its blood is always at a low temperature but that the temperature of its blood and therefore of its body is never more than one or two degrees above that of the environment and varies with the temperature of the environment. As the cold weather comes and winter approaches, frogs take to the water and burrow into the moist mud at the bottom of ponds below the frost line. Here they **hibernate** through the winter.

While hibernating the frog takes no food, being dependent during this time on the energy stored in its body as fat and glycogen. All activities are suspended except those necessary to maintain life, such as the beating of the heart. Its metabolism is much reduced, little oxygen is required, and respiration takes place entirely through the skin.

Man, on the other hand, is a **warm-blooded** animal, which really means that his body temperature remains constant and independent of the temperature of his environment. The normal temperature of the human body is approximately 98.6° F or about 37° C. Most chemical reactions go on more rapidly the higher the temperature, and this is true of most of the chemical reactions which go on within the body and constitute metabolism. Thus the metabolism of warm-blooded animals, like mammals and birds, is, in temperate climates at least, more rapid than in cold-blooded animals, and warm-blooded animals are more active.

To maintain the body temperature of an organism above that of its surroundings requires energy. Thus the energy which enters the body of an animal, locked in the chemical compounds which it absorbs and assimilates, is utilized in two ways: to maintain its body temperature and to carry on its various activities. In the frog the amount of energy which goes to maintain its body temperature is small, while in man the amount is relatively large. The human body, or that of any animal for that matter, may be looked upon as a machine which does a certain amount of work as a result of being supplied with a certain amount of fuel in the form of carbohydrates, fats, and proteins. The energy to do the work comes from the oxidation, or burning, of these materials in the body.

The amount of energy which 1 gram of one of these substances yields when oxidized or burned can be determined in an apparatus called a **calorimeter** (caloric measure), which absorbs and measures the heat generated. It is as a result of determinations in an apparatus of this kind that it is known that 1 gram of carbohydrate yields 4.1 calories, 1 gram of protein approximately the same amount, and 1 gram of fat, 9.3 calories. The calorie here referred to is the large calorie or kilocalorie which is equal to the amount of heat necessary to raise 1 kilogram of water from 15° C to 16° C. From his food it is possible to determine the total number of calories which a man takes into his body in a day or a week. If the body is a machine as far as the energy transformations in it are concerned, it ought to be possible, if there is no increase in the body weight during the time of the experiment, i.e., if there is no energy stored in the body, to account for the calories taken into it, in work accomplished.

Such experiments have been carried out on the human subject. Large calorimeters have been built in which men have lived for weeks, the amount of energy supplied to them as food carefully measured, and the amount of energy given off in the form of body heat and work also measured. One method of measuring the amount of work done is to have the man ride a stationary bicycle, the back wheel working against a brake. From the number of revolutions of the wheel and the force on the brake the amount of work done can be calculated. The results of many such experiments carefully performed with more or less elaborate apparatus have shown that, in respect to the energy transformations within it, the human body does behave like a machine.

Of considerable interest is the amount of energy needed just to main-

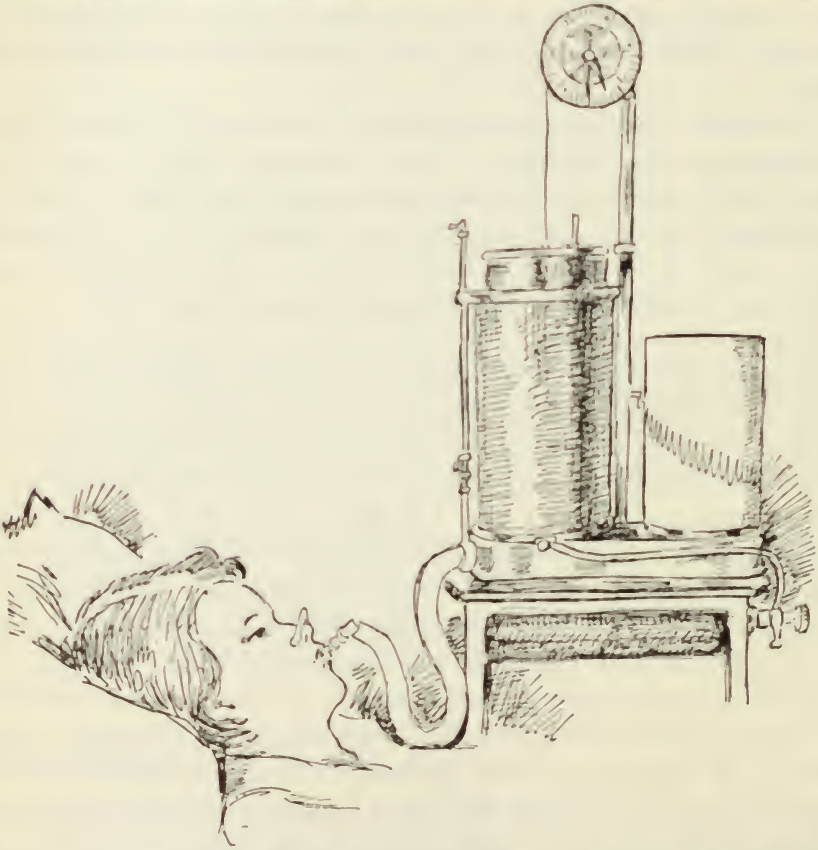


Fig. 29:6 An apparatus for the determination of basal metabolism. On the right an inverted cylindrical chamber containing air (shaded in the drawing) is hung from a pulley in another chamber with an air-tight seal. As the patient breathes in and out, the chamber falls and rises, writing a line on the revolving drum shown at the extreme right which records the decrease in volume due to the oxygen taken in by the patient and the carbon dioxide absorbed by the soda-lime in the gas chamber. From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, The Macmillan Company.

tain a person's vital activities in the resting condition, i.e., when he is doing no outside work. This, which is called the **basal metabolism,** is important in certain diseases and is a routine determination in hospitals. The determination is usually made before breakfast and with the person lying in bed. Since the energy liberated in the body is due to oxidations, the amount of energy liberated in any time can be calculated from the amount of oxygen used. The subject is made to breathe out of and into a chamber containing pure oxygen. The carbon dioxide expired by the subject is absorbed from the chamber with soda-lime. The decrease in volume of the gas in the chamber is then equal to the amount of oxygen consumed. In the case of truly basal metabolism all of the energy liberated then goes into heat. The average rate at which this heat is produced in a normal adult is 1500 to 1800 calories per day. It will be remembered that the average man requires a diet containing about 3000 calories per day. Thus in a normal man approximately one-half of the energy value of the food substances taken into his body goes to maintaining his body temperature and such essential vital activities as breathing and the beat of the heart. The other half is available for the performance of external work (Fig. 29:6).

Topical Outline of Chapter 29

1. Food substances 555
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   A. Minerals required by the body 556
   B. Vitamins 556
3. Digestion, changes undergone by the food in the mouth, in the stomach, in the small intestine, and in the large intestine 561
4. The rate of movement of materials through the alimentary canal 564
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7. General metabolism 566
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   B. Fat metabolism 568
   C. Protein metabolism 569
8. Energy changes in the body 570

Questions

1. What classes of chemical substances are necessary in a diet?
2. Name the vitamins and state the effect of the absence of each from a diet.

3. About how many calories per day does the average man require?
4. State the chemical changes occurring in the digestion of starch.
5. Discuss the changes undergone by the food in the stomach.
6. Discuss the changes undergone by the food in the small intestine.
7. Trace what happens to the various constituents of a ham sandwich when eaten by a man.
8. Where and how does the absorption of food substances occur?
9. Distinguish between anabolism and katabolism.
10. Discuss and compare protein, carbohydrate, and fat metabolism.
11. Distinguish between cold-blooded and warm-blooded. What advantages and disadvantages are there in being warm-blooded?
12. Discuss the human body as a machine for doing muscular work.

Suggestions for Further Reading

Amberson, William R., and Dietrich C. Smith, *Outline of Physiology*, F. S. Crofts & Co., New York, 1939, Chaps. XVIII, XIX, and XXV.

Best, Charles H., and Norman B. Taylor, *The Living Body, A Text in Human Physiology*, Henry Holt and Company, Inc., New York, 1938, Chaps. 4 and 5.

CHAPTER 30

The Respiratory and Excretory Systems

1. THE RESPIRATORY ORGANS OF THE FROG

The frog's blood receives oxygen and gives up carbon dioxide through its skin, the lining of its mouth, and its lungs. The frog's **skin** is abundantly supplied with blood vessels and is kept moist with mucus from mucous glands. Oxygen from the air or water surrounding the frog passes through the cells of the epidermis and of the walls of the capillaries into the blood stream, and carbon dioxide diffuses from the blood through the same structures to the air.

The lining of the **mouth and the tongue** are also abundantly supplied with blood vessels. If a frog in the usual resting position be watched, the floor of its mouth will be seen to be continually moving up and down. As its nostrils are usually open and its glottis usually closed, by this movement air is alternately drawn into and forced out of the mouth cavity. Thus the air in the mouth is continually renewed, a condition which aids respiration in the mouth.

The **glottis** of the frog opens into the cavity of a small cartilaginous box, the **larynx** or **voice box**. The larynx leads directly into the two lungs. The tissue of the lungs is exceedingly elastic, so that when inflated they look like small balloons. They differ from balloons in that the air space is divided into smaller spaces by partitions, thus increasing the surface exposed to the air (Fig. 30:1). The walls of the lungs are plentifully supplied with blood capillaries, which are separated from the air by only a very thin layer of epithelial cells. Oxygen from the air diffuses through these cells and the equally thin cells of the capillaries into the blood, and, in a similar way, carbon dioxide diffuses out of the blood.

The frog **breathes** by pumping air into its lungs and then letting the air out of them (Fig. 30:2). Attention has already been drawn to the up-and-down movement of the floor of the mouth and the effect of this in changing the air in the mouth when the nostrils are open and the glottis closed, as is usually the case. From time to time, however, the glottis is opened. When this occurs, air escapes into the mouth from

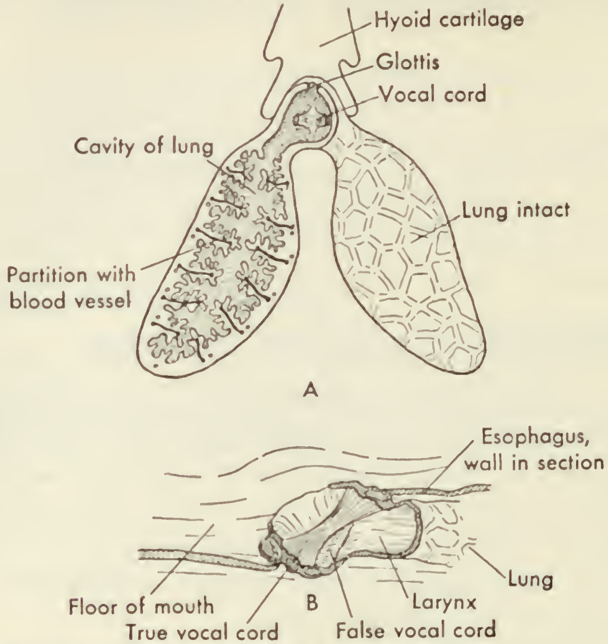
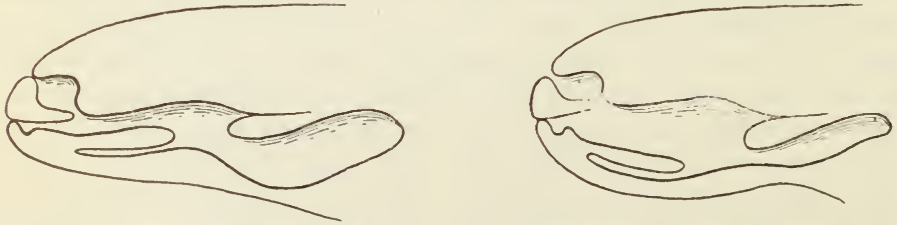


Fig. 30:1 The respiratory system of the frog. A, the lungs and larynx dissected from the ventral side. The right lung has been cut open to show the internal structure. B, a lateral dissection of the larynx made by cutting vertically through the glottis and between the lungs. The dorsal side is above, and the glottis opens toward the upper left in the figure.

the lungs owing to their great elasticity and to contractions of the muscles of the flanks. Almost immediately, however, the nostrils are closed and as the floor of the mouth is raised, air from the mouth cavity is forced



Inspiration; floor of mouth raised, external nares closed, lung expanded

Expiration; floor of mouth lowered, external nares open, lung contracted

Fig. 30:2 Respiratory movements in the frog.

through the open glottis into the lungs. Since this pumping action occurs only at intervals and the movement of the floor of the mouth goes on continuously, the air in the mouth is changed more frequently than the air in the lungs. If the mouth of a frog is held open the animal is unable to force air into its lungs and may even die of asphyxiation.

In vertebrates, the respiratory process occurs in three steps. First is **breathing,** which, strictly speaking, is not respiration and consists merely of changing the air in contact with the respiratory surface. In the case of the frog this may be the skin, mucous membrane of the mouth, or lining of the lungs. Next is **external respiration,** in which oxygen is passed into, and carbon dioxide out of, the blood. Lastly there is **internal respiration,** in which the oxygen of the blood is given up to the tissues of the body, and carbon dioxide is passed from the tissues to the blood.

The larynx contains the **vocal cords,** which are elastic folds of its walls rather than cords in the ordinary sense. There are two sets of vocal cords, the **true vocal cords,** which are responsible for the sound and determine the pitch of croaking, and the **false vocal cords,** situated behind the true vocal cords, which, although similar in structure to the true vocal cords, play no part in the frog's vocal activities. Certain muscles attached to cartilages in the larynx control the tension in the true vocal cords. When the frog croaks air is forced through the larynx between the stretched vocal cords; these go into vibration and cause the sound.

2. THE RESPIRATORY SYSTEM OF MAN

The structures associated with the nasal cavities and mouth have already been described in Chap. 28. In breathing, the air may enter either through the nostrils, **nasal breathing,** or through the mouth opening, **mouth breathing.** In nasal breathing the air enters at the nostrils and passes into the nasal cavities. From the nasal cavities it passes through the internal nares into the nasopharynx and from there into the oral pharynx. From the oral pharynx it passes through the glottis into the larynx, crossing as it does so the passageway of the food from the mouth to the esophagus. The larynx in man projects in the front of the neck as the "Adam's apple" and is easily felt as a rounded structure below the lower jaw. As in the case of the frog, the vocal cords are folds of the lining of the larynx rather than cords in the usual sense of the word. The true vocal cords are below the false vocal cords. If the finger and thumb are placed on the larynx and a vowel, such as the letter *a*, be pronounced, the vibration of the true vocal cords can easily be felt.

The lower part of the larynx leads into a long cylindrical tube, the **trachea,** which passes down through the neck in front of the esophagus and into the chest. At about the middle of the chest the trachea divides into two tubes, the **right** and **left bronchi,** leading to the right and left lungs. In the lungs the bronchi divide up into smaller tubes called **bronchioles.** The trachea, the bronchi, and larger bronchioles are rendered noncollapsible by **rings of cartilage** (Fig. 30:3). Each bronchiole ends in a structure which looks not unlike a bunch of grapes. The round grapelike projections are minute air sacs, called **alveoli,** which communicate with the enlarged end of the bronchiole. The alveoli are lined by a single layer of thin, flattened epithelial cells and surrounded by a network of capillaries. It is through the walls of the alveoli that the oxygen passes into and the carbon dioxide out of the blood. The alveoli, bronchioles, and bronchi of each lung are bound together into a compact but spongy and very elastic mass by connective tissue, which is covered by a layer of peritoneum called the **pulmonary pleura.** A similar layer of peritoneum lines the pleural cavity, the **parietal pleura.** A very small amount of fluid separates the pulmonary pleura from the parietal pleura.

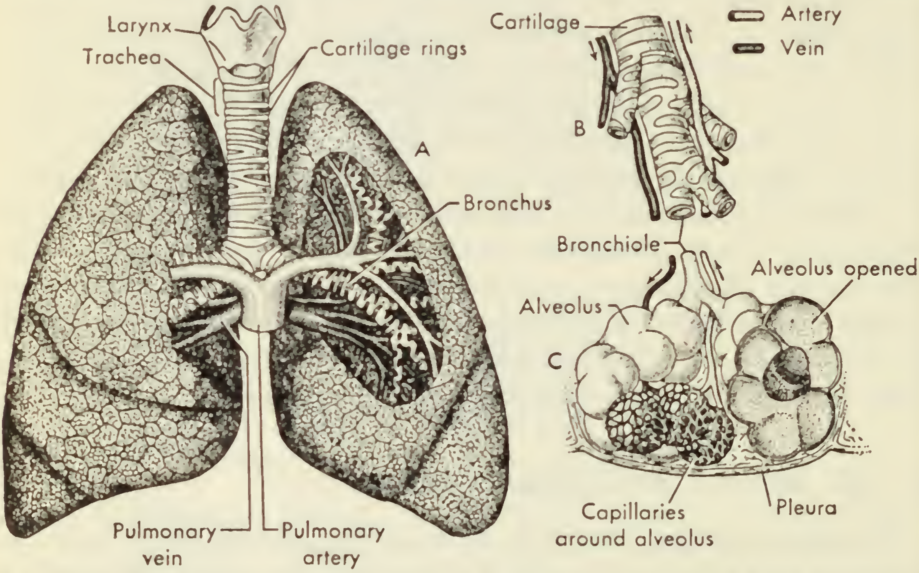
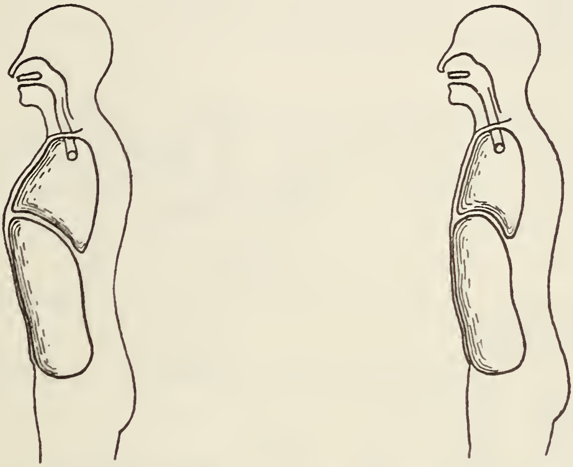


Fig. 30:3 The human respiratory system. A, larynx, trachea, and lungs in ventral view, left lung opened. B, portion of a bronchiole, with cartilages and adjacent small blood vessels. C, alveoli and capillaries. From Storer, *General Zoology*, McGraw-Hill Book Company, Inc.

There are two methods of increasing and decreasing the size of the pleural cavities and thereby drawing air into and forcing air out of the lungs (Fig. 30:4). In **diaphragmatic breathing** the muscles of the diaphragm are contracted and this dome-shaped sheet of tissue is flattened out and the floor of the thorax lowered. Since the rest of the thorax does not decrease in size, the volume occupied by the lungs is increased and air rushes into them. By a subsequent relaxation of its muscles and contraction of the abdominal muscles the diaphragm reassumes its dome shape and air is forced out of the lungs.

In **costal breathing** the ribs and sternum are drawn upward by the contraction of intercostal muscles and other muscles in the chest and neck. Since the ribs slant from the vertebral column downward and to the side, raising them increases both the width and thickness of the chest, and hence the volume occupied by the lungs. Air is therefore drawn into them. With the relaxation of the intercostal and other muscles referred to, the ribs are lowered and air is forced out of the lungs. In normal breathing both methods are employed, the diaphragmatic method tending to predominate.



Inspiration; lung volume increased, ribs raised, diaphragm lowered

Expiration; lung volume reduced, ribs lowered, diaphragm raised

Fig. 30:4 Respiratory movements in labored breathing in man.

Although we are not ordinarily conscious of the movements we make in breathing, the muscles are voluntary muscles under the control of the central nervous system, as is shown by the fact that a person can hold his breath. The rhythm of breathing is controlled by a **respiratory center** in the brain, which in turn is stimulated by the carbon dioxide in the blood. This is why in cases of asphyxiation a mixture containing carbon dioxide and oxygen and not pure oxygen is administered.

The **volume of air** which can be taken into or forced out of the lungs is easily measured by an instrument called a **spirometer.** This consists essentially of a cylinder in which the volume is measured connected with a tube ending in a mouthpiece (Fig. 30:5). The actual volumes vary considerably in different persons. When a person is sitting at rest and breathing quietly he takes in and gives out about 500 cubic centimeters at each breath. This is called the **tidal air** (Fig. 30:5). If from this resting condition of the lungs he tries to expel as much air as he can from them, the volume expelled may be about 1500 cubic centimeters. This is called the **supplemental air.** If on the other hand, starting at the resting position, he tries to inhale as much air as possible by expanding his chest, the volume inhaled will be about 2000 cubic centimeters. This is called the **complemental air.** The tidal air plus the supplemental air plus the complemental air equals the **vital capacity.** This is also the volume of air which can be expelled from the lungs when the subject starts with them fully expanded and expels all the air he is able to expel. However, even when the greatest effort is made to expel the air from the lungs there is still a considerable volume left. This is called the **residual air** and in the case under consideration would be about 1500 cubic centimeters. It thus appears that the air in the lungs is never completely changed at one time. Indeed only about one-tenth of the total volume is changed in an ordinary quiet respiration. Even in this case a good proportion of fresh air enters the alveoli. The rate of

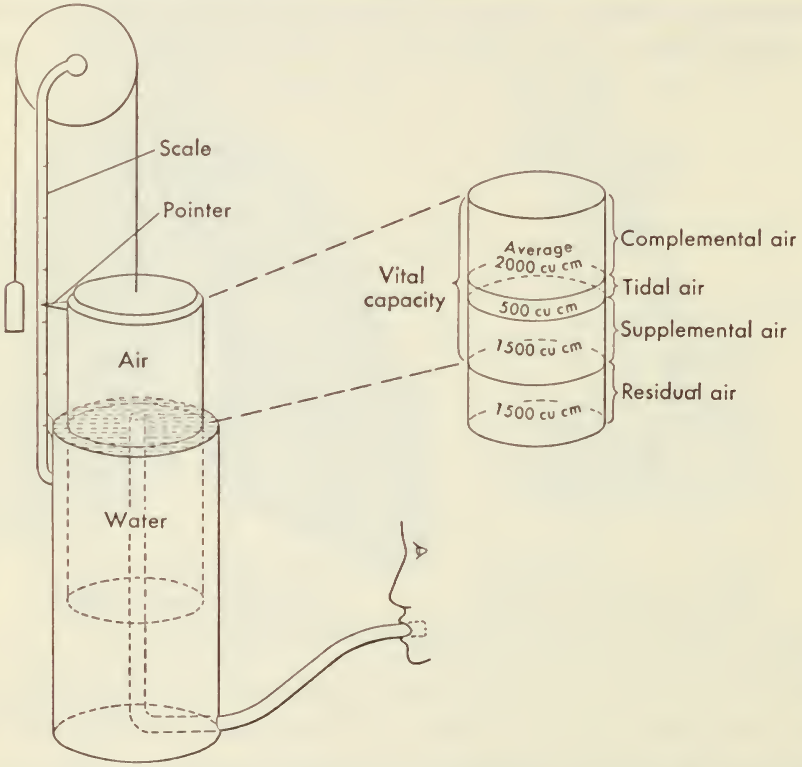


Fig. 30:5 The measurement of expired and inspired air. On the left, a spirometer; on the right, diagram showing average volumes.

respiration varies with age, position of the body, and activity. A young adult in the sitting position averages about 18 inhalations per minute.

The atmosphere contains about 21 per cent oxygen and about 0.03 per cent carbon dioxide. The air expelled from the lungs contains approximately 16 per cent oxygen and 4 per cent carbon dioxide (Table 30:1). However, people can live without great discomfort where the oxygen is equivalent to only about 12 to 13 per cent and the carbon dioxide per cent reaches 1. **Ventilation** is not so much a question of oxygen and carbon dioxide as of air conditioning, i.e., getting rid of smells, dust, and excess moisture.

TABLE 30:1. GASEOUS CONTENT OF INSPIRED AIR, EXPIRED AIR, ARTERIAL BLOOD, AND VENOUS BLOOD IN PER CENT OF VOLUME[1]

	OXYGEN	CARBON DIOXIDE	NITROGEN	OTHER GASES
Inspired air	21	0.03	78	1
Expired air	16	4.00	78	1
Arterial blood	20	40.00	1–2	
Venous blood	15	40–50	1–2	

3. THE EXCRETORY SYSTEM OF THE FROG

Excretion is the giving off of the waste products of metabolism. A substance cannot be said to be excreted unless it at one time took part in the metabolism of the organism. Thus excretion is clearly to be distinguished from defecation which refers to the passing out of the body of undigested materials from the alimentary tract. The skin, liver, and the walls of the intestine are important excretory organs but they will not receive special consideration here.

The **kidneys** of the frog are two reddish, flat, oval bodies lying against the dorsal body wall about midway between the ends of the abdominal cavity. They are covered only on their ventral sides by the peritoneum and are thus outside the body cavity (Fig. 27:12). From the lateral side of each kidney, near the posterior end, runs a tube called the **ureter** which opens into the cloaca. The urinary bladder is an outgrowth from the ventral side of the cloaca and is not connected with the ureters (Fig. 30:6).[2]

The internal structure of the kidney is seen best in microscopic sections. The ureter is continued through the substance of the kidney to its anterior end. A transverse section of the kidney shows transverse **collecting tubules** running across the dorsal portion of the kidney (Fig. 30:7). With these are connected numerous fine tubules running to the ventral portion. These fine tubes, called **uriniferous tubules,** run from the collecting tubules to the ventral side of the kidney where they make a few coils and then run dorsally again to the vicinity of the collecting tubules, where, after making a few more coils, they turn to run again to the ventral side of the kidney. Here each of the uriniferous tubules ends in a slight enlargement, called a **renal capsule.** Into the renal capsule projects a small tangled mass of blood capillaries called a **glomerulus.** The glomerulus and renal capsule together form the **Malpighian body** or **renal corpuscle.** The excretory unit of the kidney, sometimes called a **nephron,** consists of a uriniferous tubule and a renal capsule.

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[1] Data from W. D. Zoethout and W. W. Tuttle, *Textbook of Physiology*, C. V. Mosby Company, St. Louis, 1940.

[2] The kidney and ureter of the frog are not homologous to the kidney and ureter of mammals, including man, since their embryological development is different. The frog's kidney is a mesonephros and its duct a mesonephric duct.

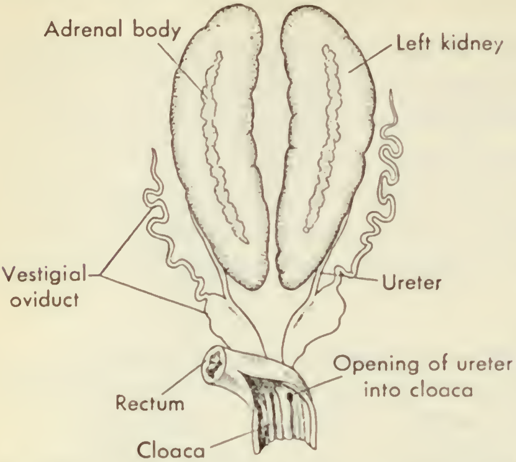

Fig. 30:6 The excretory system and associated organs of the male frog. Urinary bladder is not shown; it opens into the ventral side of the cloaca.

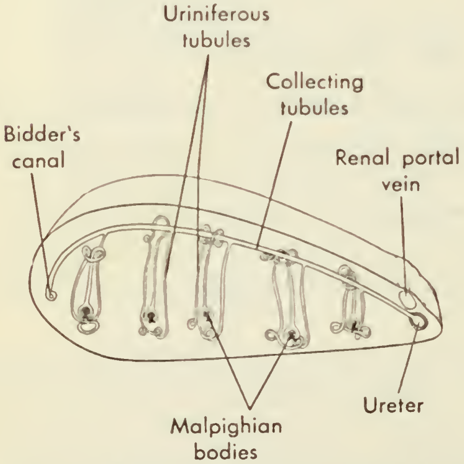

Fig. 30:7 Diagram of a cross section of a frog's kidney. Bidder's canal, present in some European frogs, is apparently absent in the common American species *Rana pipiens*. After S. J. Holmes, *The Biology of the Frog*, The Macmillan Company.

From the uriniferous tubules the urine passes into the collecting tubules and from these to the ureter. The ureters, as already stated, open into the cloaca and are not connected with the urinary bladder. Since the anus of the frog is usually kept closed by its sphincter muscles the urine backs up from the cloaca into the bladder where it is stored.

In the tailed amphibia, which represent less specialized animals lower in the scale of evolution, ciliated funnel-shaped openings, called **nephrostomes,** occur on the ventral surfaces of the kidneys and lead from the coelom into the uriniferous tubules. In this case there is a striking correspondence between the nephridia of an earthworm, which, it will be remembered, open into the coelom, and the uriniferous tubules of the amphibia, with the difference that the uriniferous tubules are connected with the ureter while the nephridia of the earthworm open directly to the exterior.

4. THE EXCRETORY SYSTEM OF MAN

As in the frog, the skin, lungs, liver, and the mucosa of the intestine perform excretory functions. We will consider first, however, the **kidneys** whose function is, so far as is known, entirely excretory (Fig. 30:8). The shape of the mammalian kidney is so characteristic that the term "kidney-shaped" is in common use. The kidneys in man occupy positions in the body corresponding to the positions occupied by the kidneys in the frog. Like them, they lie against the dorsal body wall, covered only on their

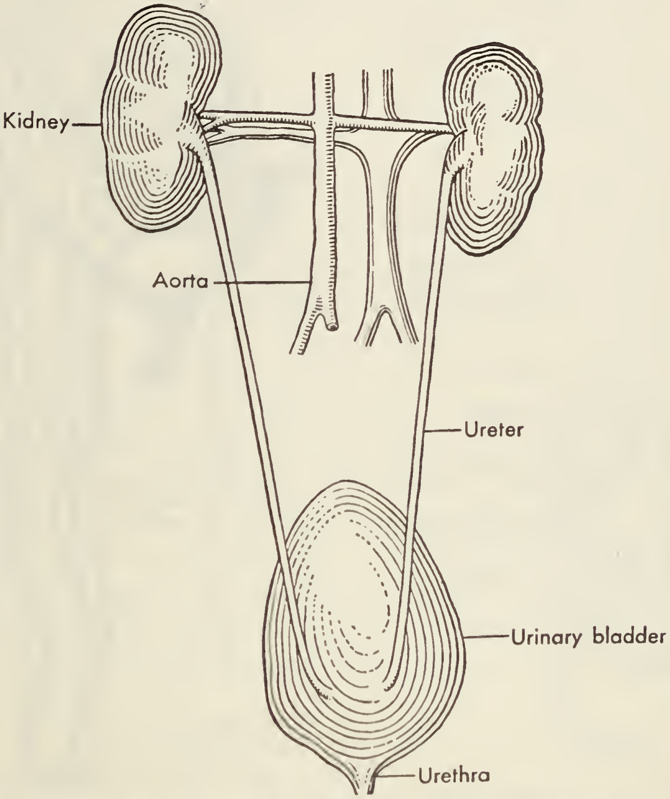

Fig. 30:8 The human urinary system viewed from behind. From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, The Macmillan Company.

ventral sides by peritoneum. The notch in the side of each kidney, called the **hilus,** is turned toward the vertebral column. A **ureter** emerges from each kidney at the hilus and passes down along the dorsal body wall to the urinary bladder into the posterior wall of which it opens. The **urinary bladder** lies in the pelvic cavity in front of the rectum. It is a muscular sac which, when distended with urine, is oval in shape. The lower portion of the bladder narrows to form a tube, the **urethra,** which opens on the exterior of the body and through which the urine is voided.

A longitudinal section of a kidney shows that the ureter expands into a funnel-shaped cavity, called the **pelvis of the kidney,** which occupies the central portion (Fig. 30:9). The solid portion of the kidney is differentiated into an outer **cortical substance** and an inner or **medullary substance. Malpighian bodies,** similar to those of the frog kidney, occur in the cortical portion and give to it a granular appear-

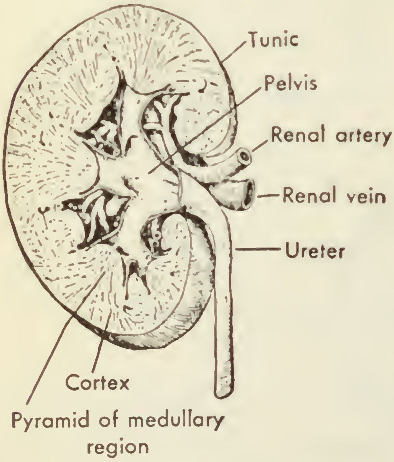

Fig. 30:9 A human kidney bisected to show internal structure. From L. L. Woodruff, *Animal Biology*, The Macmillan Company.

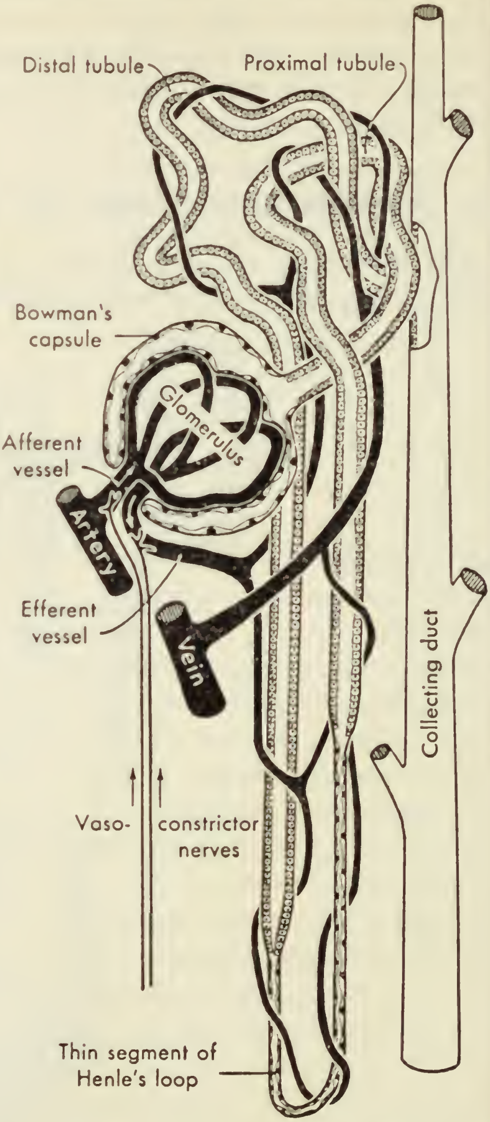

Fig. 30:10 A diagram showing a single secretory unit of the kidney. From W. R. Amberson and D. C. Smith, *Outline of Physiology*, F. S. Crofts & Company.

ance. Blood comes to the capillaries of the glomerulus in an artery and leaves in a vein. The artery is in this case larger than the corresponding vein because the volume of blood entering the glomerulus is greater than the volume leaving it by the volume of the liquid passed out into the capsule. As in the frog, a **uriniferous tubule** extends from each Malpighian body to join a **collecting tubule** (Fig. 30:10). In man the uriniferous tubule is differentiated into three portions called respectively the proximal convoluted tubule, loop of Henle, and distal convoluted tubule. The **proximal convoluted tubule** is a much-coiled portion located in the cortex of the kidney and directly connected with the Malpighian body. The **loop of Henle** is a long U-shaped tubule which extends from the proximal convoluted tubule into the medullary portion of the kidney and returns to the cortical portion where it unites with the distal convoluted tubule. The **distal convoluted tubule** contains several irregular coils in close proximity to those of the proximal convoluted tubule. It connects with the collecting tubule. The collecting tubules join to form **excretory tubes** which open by pores on conical elevations of the kidney tissue called **papillae** which project into the pelvis of the kidney. The excretory unit or nephron consists of the Malpighian body, the proximal convoluted tubule, the loop of Henle, and the distal convoluted tubule. In going from the uriniferous tubules to the exterior the urine takes the following course: uriniferous tubules to collecting tubules to excretory tubules to pelvis of kidney to ureter to bladder and out through the urethra.

The urine normally contains about 95 per cent water, but the amount varies greatly according to the amount of liquid taken by the person and the amount of water lost in perspiration, through the skin, which may be equal in amount to that given off by the kidneys. The other 5 per cent consists of soluble salts, of which somewhat over 1 per cent are inorganic and somewhat under 4 per cent are organic, chiefly urea. Urea, $CO(NH_2)_2$, is the chief nitrogenous waste product of the body; it occurs also in perspiration.

5. THE EXCRETION OF THE URINE

Much of our knowledge concerning the function of the different parts of the **nephron** or excretory unit of the kidney is the result of investigations carried out on the kidney of the frog and the mudpuppy (*Necturus*), also an amphibian. Recently the technique has been perfected and applied to the mammalian kidney, so that there is now fairly accurate and complete information concerning the excretion of the urine. In one of the most fruitful methods of experimentation fine capillary tubes are introduced by means of a micromanipulator in the Malpighian capsule and at various points into the uriniferous tubule. By means of these fine tubules liquid is withdrawn for measurement and microchemical analysis. In this way it can be shown that two quite different processes occur in the formation of the urine. The first of these occurs in the Malpighian capsule, the second in the uriniferous tubule.

The **Malpighian body** acts as a **filter** in which the blood corpuscles and blood colloids, chiefly proteins, are held back and the plasma, including the blood salts, urea, uric acid, and water pass through the walls of the capillaries and the endothelium covering the glomerulus into the cavity of the capsule. Filtration requires a difference of pressure. In this case the difference in pressure is that between the blood pressure in the capillaries and the pressure in the liquid in the capsule. It has been shown that, other factors remaining constant, an increase in the blood pressure causes an increase in the volume of urine. That the walls of the capillaries and the endothelium act as filter has been shown by comparing the composition of the plasma in the blood with the fluid in the capsule by means of the technique outlined in the previous paragraph. In the filtration process the capillary walls and the endothelium act as living membranes. If they are injured the filtrate is different. Proteins are then found in the urine.

The **uriniferous tubules** are mainly concerned with the **reabsorption** of various materials from the filtrate as it passes through them. That water is reabsorbed is shown by the fact that calculations reveal that the total amount of filtrate formed in the kidney by the Malpighian bodies in an adult is about 200 liters per day while the actual amount of urine passed in the same period is only about 1½ liters. Not only water is reabsorbed by the tubules. Analysis of the fluid in the Malpighian capsule shows that glucose is present there in approximately the same concentration as in the blood, while glucose is practically absent from the fluid

TABLE 30:2. COMPARISON OF CONCENTRATION OF SUBSTANCES IN BLOOD PLASMA AND IN URINE[1]

	PER CENT	
	BLOOD PLASMA	URINE
Water	90–93	95
Proteins, fats, and other colloids	7–9	0
Glucose	0.1	0
Sodium	0.30	0.35
Chloride	0.37	0.60
Potassium	0.02	0.15
Urea	0.03	2.00
Uric acid	0.004	0.05

[1] Data from W. R. Amberson and D. C. Smith, *Outline of Physiology*, F. S. Crofts & Co., New York, 1939.

in the distal tubule, except in those cases where there is an excess of glucose in the blood, when it may appear in the urine. Chlorids are also reabsorbed. The same is true of bicarbonates. The reabsorption of the latter with the absence of their buffering effect is the chief reason for acid reaction of the urine. While urea is not reabsorbed in the frog it appears that in mammals a small proportion of the urea may be reabsorbed. Filtration and reabsorption is, however, not the whole story. There is good evidence that creatinine, the anhydride of creatine referred to already in considering muscle metabolism, is secreted by the urinary tubules from the blood into the urine. The accompanying table shows the relative concentrations of various substances in the plasma and urine (Table 30:2).

Although excretion is the most obvious function of the kidney it plays a perhaps equally important role in another function which is carried out by a number of parts of the body conjointly, viz., the maintenance of a constant composition of the blood and through it a constant environment for the cells of the body. The maintenance of this constant environment is discussed in the next chapter.

Topical Outline of Chapter 30

1. The respiratory organs of the frog 575
2. The respiratory system of man 577
3. The excretory system of the frog 581
4. The excretory system of man 583
5. The excretion of the urine 585

Questions

1. Compare the methods of breathing of a frog and a man.
2. Distinguish between breathing, external respiration, and internal respiration.
3. Trace the path which a molecule of oxygen would travel in going from the atmosphere into the blood of a man and state the forces which move it.
4. Compare the kidneys of a frog with those of a man.
5. In what part or parts of the kidney does the actual excretion occur?

Suggestions for Further Reading

Amberson, William R., and Dietrich C. Smith, *Outline of Physiology*, F. S. Crofts & Co., New York, 1939, Chaps. XVIII, XIX, and XXV.

Best, Charles H., and Norman B. Taylor, *The Living Body, A Text in Human Physiology*, Henry Holt and Company, Inc., New York, 1938, Chaps. IV and V.

Kimber, Diana C., Carolyn E. Gray and Caroline E. Stackpole, *Textbook of Anatomy and Physiology*, The Macmillan Company, New York, 1935, Chaps. XVII and XXI.

CHAPTER 31

The Circulatory System

1. THE BLOOD OF THE FROG

The blood is a living tissue. It differs from other tissues in that the matrix or intercellular substance is liquid. This liquid portion is called the plasma. The cells, or corpuscles, as they are called in the blood, are of different kinds. The red corpuscles, or **erythrocytes,** are oval in shape and nucleated in the frog (Fig. 4:15). Their function is to carry the red respiratory pigment, called **hemoglobin.** The white corpuscles, or **leucocytes,** are less numerous and, in the frog, smaller than the red corpuscles; their nuclei are relatively large. Unlike the red corpuscles which retain a fixed shape, the white corpuscles are capable of amoeboid movement. Certain of them have as a function to ingest foreign bodies in the blood, including bacteria, and are hence called **phagocytes** (Gr. *phagein*, to eat + *kutos*, cell). In addition there occur **spindle cells,** called also **thrombocytes,** which are smaller than either the red or the white corpuscles. These contain a substance which causes the clotting of the blood when they disintegrate.

2. THE BLOOD OF MAN

Human blood contains practically the same elements as the blood of the frog, namely, plasma, red corpuscles, white corpuscles, and **blood platelets** or thrombocytes which are small, irregular, enucleate bodies comparable to the spindle cells of the frog (Fig. 31:1). The red corpuscles or erythrocytes are biconcave circular discs, 0.007 millimeter in diameter, which is about one-third the diameter of the frog's red corpuscles. The red corpuscles of a man, whale, elephant, and mouse do not differ in diameter by more than about 0.0025 millimeter. As seen in the circulating blood they are without nuclei, although they develop from nucleated cells in the bone marrow and subsequently lose their nuclei. The white corpuscles, which are greater in diameter than the erythrocytes, are nucleated and of a number of different kinds. The most numerous are the **polymorphonuclear leucocytes** in which the nuclei are irregular in shape and divided into a number of lobes. The polymorphonuclear leucocytes normally comprise 60 to 75 per cent of the white corpuscles, but their number may be greatly increased in certain pathological conditions where pus is formed. It is chiefly these corpuscles which act as phagocytes.

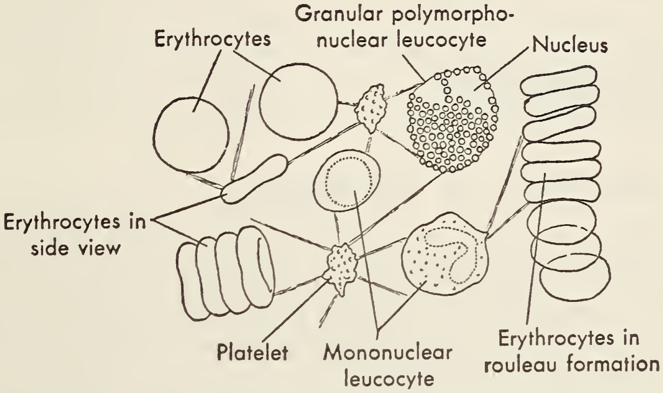
Granular polymorphonuclear leucocyte
Erythrocytes
Nucleus
Erythrocytes in side view
Platelet
Mononuclear leucocyte
Erythrocytes in rouleau formation

Fig. 31:1 Human blood corpuscles and platelets. The strands extending between the corpuscles and platelets are of fibrin formed when coagulation takes place. Platelet is another term for thrombocyte.

One cubic millimeter of normal blood contains approximately 5,000,000 red corpuscles and 5000 to 10,000 white corpuscles, and it takes about 25 or 30 cubic millimeters to make one good-sized drop of blood. Put in another way, if human beings were blood corpuscles the population of the world would be contained in about 10 or 15 drops. The blood of a man forms from 5 to 7 per cent of his total weight, and it has been estimated that a man weighing 68 kilograms (150 pounds) has about 25×10^{12} or 25,000,000,000,000 red corpuscles.

The life span of a red corpuscle in the circulation is comparatively short, about 2 to 3 weeks. New blood corpuscles develop in special blood-forming tissue in the marrow of the bones.

The **plasma** of the blood resembles protoplasm in its chemical composition, although not in structure (Table 31:1). This is not surprising since its function is to supply to cells the materials to build up new protoplasm and repair that which has broken down. It contains small amounts of a large number of enzymes, hormones, and vitamins. In consequence there may occur in it many of the katabolic processes which occur in cells. This does not include respiration which is limited to living cells. The reaction of the plasma is slightly alkaline (pH 7.4 to 7.7) and is slightly more alkaline than the whole blood (pH 7.2 to 7.4). The composition of the plasma is shown in Table 31:1.

TABLE 31:1. COMPOSITION OF 100 GRAMS OF HUMAN BLOOD PLASMA

	GRAMS
Water	90–92.
Solids	
Proteins	7–9.
Salts	1.
Lipides (fats and fatty substances)	0.1–0.6
Carbohydrates, chiefly glucose	0.2–0.3

3. THE FUNCTIONS OF THE BLOOD

TRANSPORT OF OXYGEN. The color of the red corpuscles is due to a substance called **hemoglobin** which is present in large quantities dissolved in the cytoplasm. Hemoglobin is a protein which contains iron, in addition to the other elements present in proteins, and is characterized by the ease with which it combines with oxygen. Due to the presence of hemoglobin the blood is able to carry seventy times as much oxygen as it would if it carried only the oxygen dissolved in the plasma. In the lungs the oxygen from the air passes through the thin epithelial walls of the alveoli and the walls of the capillaries into the plasma. From the plasma it passes into the red corpuscles and there is combined with hemoglobin. When the blood reaches capillaries in tissues, which are poor in oxygen due to oxidations going on in them, the hemoglobin gives up its oxygen through the plasma and the walls of the capillaries to the tissues.

THE TRANSPORT OF CARBON DIOXIDE. Most of the carbon dioxide transported from the tissues to the lungs is carried in the plasma of the blood in the form of sodium bicarbonate.

THE TRANSPORT OF FOOD MATERIALS. All of the products of digestion which are absorbed through the intestinal wall find their way into the blood and are carried in the plasma until taken up and used by tissue cells. Although relatively large amounts of these substances may be digested and absorbed, their concentration in the blood is low and is maintained practically constant. Thus the amount of **glucose** in the blood is about 0.1 per cent, and of **fat** about 0.2 per cent, and the amounts of these substances fluctuate only within narrow limits. Amino acids are always present in small but practically constant amounts.

THE TRANSPORT OF WASTE MATERIALS. Waste materials such as urea, uric acid, and a number of other nitrogenous substances are transported in the blood from their seat of origin to the kidneys or the skin where they are excreted.

THE TRANSPORT OF OTHER SUBSTANCES. Many other substances, such as enzymes, hormones, and immune bodies, including antitoxins which neutralize bacterial poisons, are carried in the blood.

THE EQUALIZATION OF THE BODY TEMPERATURE. The blood vessels function as a very efficient and widely distributed hot-water heating system for the body. The blood as it courses through the tissues carries the heat from parts of the body where it is being generated, such as the muscles, to the more superficial and cooler parts, maintaining an even temperature throughout. The temperatures of the different parts of the body seldom vary by more than one or two degrees Fahrenheit.

4. THE CLOTTING OF THE BLOOD

When a blood vessel is ruptured and bleeding occurs the flow of blood is normally stopped by the contraction of the walls of the vessel and the formation of a **clot.** When a clot of blood is examined under a microscope it is found to contain a tangled mass of fine fibrils. The substance of which these fibrils consist, called **fibrin,** is formed from a protein called **fibrinogen** normally in the plasma. A clot is formed when blood comes in contact with the air or foreign material such as a piece of cloth, metal, or glass. The transformation of fibrinogen into fibrin is somewhat complicated. It is initiated by the breakdown of the platelets or thrombocytes which liberates a substance which starts a series of reactions the end result of which is the formation of fibrin. If a quantity of blood is placed in a vessel the clot will separate out as a dark red mass floating in a light-colored liquid called the **serum.** The serum consists of the plasma minus the corpuscles, which are caught in the meshes of the clot, and the substances which form the fibrin.

5. BLOOD TYPES

In the case of blood transfusion, to be discussed in the next section, it is found that blood cannot ordinarily be transfused without danger between any two persons taken at random. The donor, who gives the blood, and the recipient, who gets the transfusion, must belong to certain types. The situation is best explained by assuming that the red corpuscles form **agglutinating substances** which agglutinate, or cause the massing together, of certain **agglutinable substances** in blood plasma. There are believed to be two agglutinating substances usually indicated by A and

B, and two corresponding agglutinable substances indicated by a and b. The blood of the donor must not contain an agglutinating substance for which there is an agglutinable substance in the receiver's blood. Based on the agglutinating and agglutinable substances, **four types** of human individuals occur. According to the terminology of Landsteiner (International) the groups are designated according to the agglutinating substances present in the individual as AB, A, B, and O. According to the Moss terminology the same groups are numbered with roman numerals, respectively, I, II, III, and IV (Table 31:2). The blood type of an individual is inherited and remains the same throughout life. Blood types similar to those of man occur in the anthropoid apes. The blood of many other mammals also shows blood types.

TABLE 31:2. TYPES OF INDIVIDUALS BASED ON AGGLUTINATING AND AGGLUTINABLE SUBSTANCES IN THE BLOOD

TYPE OF INDIVIDUAL		AGGLUTINATING SUBSTANCES IN RED CORPUSCLES	AGGLUTINABLE SUBSTANCES IN PLASMA
LANDSTEINER	MOSS		
AB	I	A and B	Neither a nor b
A	II	A only	b only
B	III	B only	a only
O	IV	Neither A nor B	a and b

When a blood transfusion is to be made the blood type of the recipient must be determined, if not already known from a previous determination, and the donor must be chosen so that his blood will not agglutinate that of the recipient. The results of blood transfusion between individuals of the different blood types are shown in Table 31:3. It will be noted that an individual of type AB can receive blood from any donor and that an individual of type O may act as donor to a recipient of any of the four types. Compatible donors and recipients are shown in Table 31:4.

TABLE 31:3. RESULTS OF BLOOD TRANSFUSION BETWEEN INDIVIDUALS OF VARIOUS TYPES

			BLOOD TYPE OF DONOR			
			AB	A	B	O
			o	b	a	ab
BLOOD TYPE OF RECIPIENT	AB	o	OK	OK	OK	OK
	A	b	Agglutinates	OK	Agglutinates	OK
	B	a	Agglutinates	Agglutinates	OK	OK
	O	ab	Agglutinates	Agglutinates	Agglutinates	OK

OK indicates a combination in which agglutination will not occur and which is therefore suitable.

TABLE 31:4. COMPATIBLE DONORS AND RECIPIENTS

RECIPIENT	DONOR
AB	Any type
A	O or A
B	O or B
O	O

O is universal donor
AB is universal recipient

6. BLOOD TRANSFUSION AND PLASMA ADMINISTRATION

Blood transfusion is not a new idea. However, two difficulties were early encountered. One of these was due to the existence of the blood types as already explained. This difficulty was overcome by typing the blood of the recipient and the donor where a transfusion was to be made. The discovery that blood could be kept from clotting by adding a small quantity of sodium citrate did away with the necessity for direct transfusion from one person to another and led to the establishment of **blood banks** where blood of different types can be kept ready for immediate use. Since the function of the red corpuscles is chiefly or entirely respiratory, and there are normally many more of these in the blood than are required for ordinary respiration, when the loss of blood has not been too great many of the benefits conferred by a transfusion of whole blood may be obtained by the administration of **blood plasma only,** i.e., blood from which the red corpuscles have been taken and which has been prevented from clotting. Further, the plasma may be dried for storage and transportation and sterile distilled water added when it is to be administered. This has the added advantage that agglutination does not occur with plasma administration and it is therefore not necessary to know the blood type of either the recipient or the donor. This technique was first used in 1940. By means of it and the generosity of blood donors millions of lives have been saved.

7. KINDS OF BLOOD VESSELS

The blood of vertebrates circulates in a closed system of vessels. These vessels consist of arteries, veins, and capillaries. The blood is carried away from the heart and to the tissues in the arteries. In the tissues it passes from the arteries through capillaries to the veins. In the veins the blood passes back to the heart. The blood is always at a higher pressure in the arteries than in the veins. Arteries always have thicker and more muscular walls than veins of comparable size (Fig. 31:2). The walls of all of the blood vessels are elastic, so that when blood is forced into them they expand. The capillaries are exceedingly small tubes, usually not greater and often less in diameter than the red corpuscles, so that the latter have to squeeze through by bending or twisting. Their walls consist of a single layer of thin, flattened epithelial cells (Fig. 31:3). It is through the walls of the capillaries that all transfer of materials between the blood and the tissues occurs.

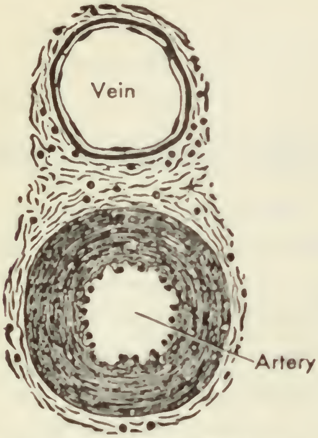

Fig. 31:2 Transverse section through a small artery and a small vein, showing the relative difference in the thickness of their walls. After Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, The Macmillan Company.

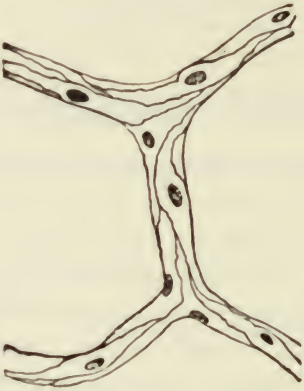

Fig. 31:3 Fine capillaries from the mesentery. The small, dark, oval bodies are the nuclei of the epithelial cells. From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, The Macmillan Company.

8. THE CIRCULATION IN A SIMPLE VERTEBRATE

It will help us to understand the circulation of the blood in the frog and man if we study it first in a simple vertebrate, such as the dogfish or shark (Fig. 31:4). Like all fishes the dogfish breathes by means of gills. The **gills,** which are highly vascular organs, line the walls of slits, **gill clefts,** which lead from the cavity of the **pharynx** sidewise on either side to the exterior. Water is continually taken into the mouth cavity and passed through the pharynx and out at the gill clefts. Thus the gills are continually bathed in a current of fresh water. In the dogfish there are six clefts, although the first (spiracle) is small and its gill rudimentary. For purposes of description the gill clefts are numbered from anterior to posterior. The masses of tissue between the gill clefts really form the side walls of the pharynx and are called **gill arches.** The first of these arches is in front of the first cleft and forms the lower jaw. For this reason it is called the **mandibular arch.**

The **heart** of the dogfish is located ventral to the posterior end of the pharynx in a position which corresponds somewhat to our throat. A large vessel, **the ventral aorta,** leaves the heart and runs forward under the pharynx. This vessel gives rise to five pairs of arteries called **afferent branchial arteries** which run into the gill arches and take the blood to the gills. The afferent branchial arteries end in capillary networks in the gills. As the blood passes through these capillaries it is separated by only two thin layers of cells from the current of water which is maintained over the gills. Oxygen dissolved in this water passes through the walls of the capillaries into the blood and carbon dioxide from the blood passes out to become dissolved in the water. From the capillaries of the gills the aerated blood passes into vessels called **efferent branchial arteries,** corresponding to the afferent branchial arteries. The efferent branchial arteries lead into a large artery called the **dorsal aorta,** which runs dorsal to the pharynx. In the dogfish there are five pairs of afferent and five pairs of efferent branchial arteries running in the second, third, fourth, fifth, and sixth gill arches.

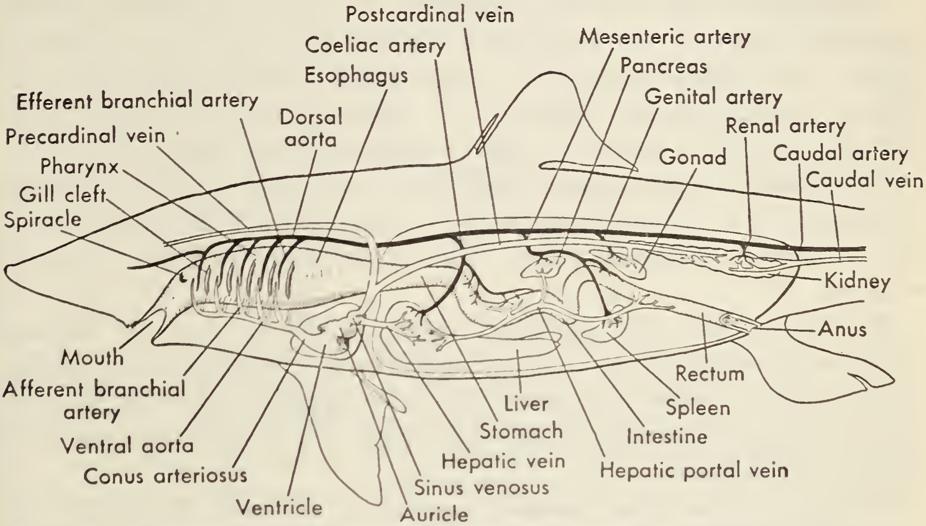

Fig. 31:4 Diagrammatic side view of the circulatory system of a dogfish. The arteries, except the ventral aorta and the afferent branchial arteries, are in solid black, the veins in outline.

The dorsal aorta runs posteriorly through the body cavity and into the tail. On its way it gives rise in succession to a **coeliac artery** to the stomach and liver, a **mesenteric artery** to the intestine and pancreas,

genital arteries to the gonads, and **renal arteries** to the kidneys, besides arteries to the muscles of the body wall and fins. In these various organs the arteries lead into capillaries putting the blood in close contact with the tissues so that exchanges of materials, such as those outlined in the two previous chapters, take place. From the capillaries the blood is collected into veins which take it back to the heart.

The **caudal vein** takes the blood from the tail to the kidneys. There it passes into capillaries. The kidney thus receives blood by two different routes — the caudal vein and the renal arteries. Blood is taken from the kidney, gonads, and the muscles of the trunk by two large paired veins, one on either side of the body, called the **postcardinal veins.** Two similar veins, called the **precardinal veins,** collect the blood from the anterior of the body. The precardinal and postcardinal veins join on each side to form **common cardinal veins** which open together into the **sinus venosus.**

The blood from the digestive tract is collected into an **hepatic portal vein** which breaks up into capillaries in the liver. After passing through these capillaries it passes into the **hepatic vein** which opens into the common cardinal veins where they join to open into the sinus venosus of the heart.

Bearing in mind that materials can enter or leave the blood only when it is passing through capillaries, the course of the blood through the body of the dogfish may be traced somewhat as follows: The blood is pumped by the heart through the ventral aorta into the gills. There in capillaries it receives oxygen and gives off carbon dioxide. From the gills it passes to the dorsal aorta which is the main vessel distributing blood to all parts of the body excepting the head region. In the various tissues of the body these arteries lead into more capillaries, where exchanges of materials occur depending on the activities of the particular tissues. Everywhere oxygen and food materials pass out of the blood into the tissues and everywhere carbon dioxide and waste materials pass from the tissues into the blood. Blood is taken away from this second series of capillaries in veins. Some of these veins, like those from the head region, the body muscles, and the fins go directly to the heart; the veins from the intestinal tract go to capillaries in the liver to which organ most of the sugar absorbed from the digestive tract is transferred; and lastly the veins from the tail carry blood to capillaries in the kidneys where it is relieved of nitrogenous waste before it passes in the postcardinal veins to the heart. While the blood may take various pathways in its circuit from the heart through the body back to the heart, it always passes through the capillaries of the gills after leaving the heart and is therefore always supplied with oxygen.

The **action of the heart** in pumping the blood through the circulatory system can be easily understood by comparing the system with a somewhat simpler mechanical arrangement. Imagine a circular rubber tube (Fig. 31:5) similar to a bicycle tire in which two valves, *a* and *b*, are arranged so that water can flow to the left but not to the right. When the tube is squeezed between *a* and *b* the pressure will close the valve at *b* and open that at *a*. Water will then flow out at *a* and cause the rest of the tube to expand. If now the pressure is released from the portion of the tube between *a* and *b*, the valve at *a* will close, owing to the back pressure from the expanded portion of the tube and the valve *b* will be opened by the same pressure and water forced into the portion between *a* and *b*. Thus by alternately tightening and relaxing one's grip on the portion of the tube between *a* and *b* water may be made to flow round the tube in a clockwise direction.

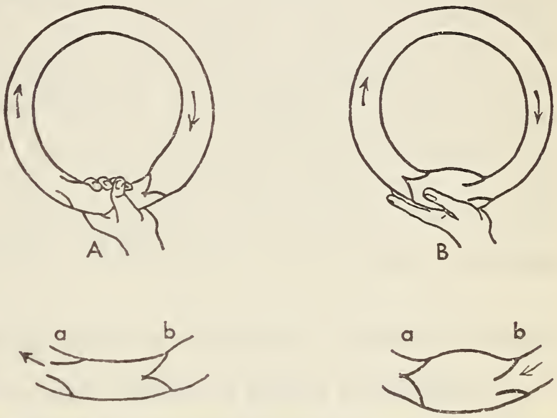

Fig. 31:5 Diagram to explain the pumping action of the heart and its effect on the circulation. When the portion between the two valves, *a* and *b*, is reduced in diameter, water is forced to the left through valve *a* causing the rest of the tube to expand, A. When the pressure on the part between *a* and *b* is released water flows in through the valve *b*, due to the elasticity of the tube, B.

The portion of the tube between *a* and *b* corresponds to the heart and its contraction to the heart beat. The flow of the water through the rest of the tube, which corresponds to the circulation of the blood, is not an even flow, but consists of a regular series of spurts, which correspond to the pulse.

To make this simple experiment simulate more nearly what goes on in the circulation of the blood in the dogfish we must have, in place of a single contracting portion of the tube with a valve at either end, four such portions, separated by three valves. Furthermore we must make the successive portions of the tube contract in succession as do the corresponding parts of the heart.

The **heart** of the dogfish is really a single tube with a succession of enlargements separated by valves. The enlargements named from posterior to anterior, i.e., in the order in which the blood passes through them, are sinus venosus, auricle, ventricle, and conus arteriosus. The **sinus venosus** is a thin-walled sac which receives the blood from the veins and passes it on to the **auricle,** through the **sinuauricular aperture.** This aperture is guarded by a pair of flaplike **valves** which prevent the blood from flowing back into the sinus venosus from the auricle. The auricle which has slightly thicker walls than the sinus venosus passes the blood to the **ventricle** through the **auriculoventricular aperture.** This aperture is also guarded by two flaplike **valves.** The ventricle, which is pear-shaped and has thick muscular walls, by its contraction forces the blood into the **conus arteriosus.** The conus arteriosus contains valves which, instead of consisting of pairs of flaps, consist of three flaps called **semilunar valves** which come together to close the passage.

9. THE ARTERIAL SYSTEM OF THE FROG

The **tadpole of a frog** resembles a fish in many ways. Like a fish it breathes by means of gills which are supported by gill arches separated by gill clefts. In the tadpole at the time of hatching there are indications of six pairs of gill clefts corresponding to those of the dogfish. Only three of these, the third, fourth, and fifth, persist and become functional. In relation to these clefts are four pairs of afferent and efferent branchial arteries, running in the third, fourth, fifth, and sixth arches and therefore corresponding to the last four pairs of afferent and efferent branchial arteries in the dogfish (Fig. 31:6). The heart of the embryo tadpole is

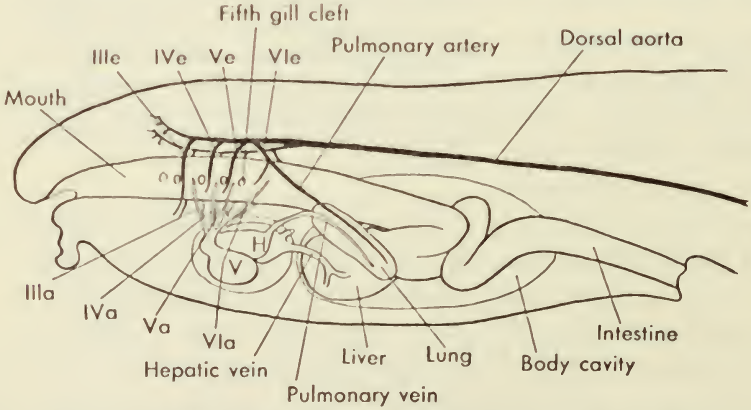

Fig. 31:6 Diagram of the circulation in the anterior end of a frog tadpole. The first gill cleft (dotted in the figure) appears only in the embryo. III*a*–VI*a*, afferent branchial arteries; III*e*–VI*e*, efferent branchial arteries. V, ventricle, H, left auricle.

not unlike that of the dogfish and consists of a sinus venosus, an auricle, a ventricle, and a conus arteriosus. The circulation of the blood through the body of the embryo follows a scheme similar to that outlined for the dogfish.

The vascular system becomes modified when the lungs develop in the tadpole; when this occurs pulmonary arteries develop as branches of the last, or sixth pair, of efferent branchial arteries. With the development of lungs and pulmonary arteries changes in the heart occur. The single auricle becomes divided into **right** and **left auricles.** The sinus venosus which, as in the dogfish, receives the blood returning from the various organs of the body, remains connected with the right auricle, while the veins which bring the blood from the lungs, called the **pulmonary veins,** open directly into the left auricle (Fig. 31:7).

When the tadpole changes into a frog it loses its gills and further changes occur in the arterial system. Of the four pairs of afferent and efferent branchial arteries, three, those of the third, fourth, and sixth arches, remain and become incorporated in the arterial system of the frog. In these pairs the efferent and afferent arteries in each arch fuse to form continuous arteries. These are the arteries running in the third, fourth, and sixth arches. The arteries of the third arch become the **carotid arches** which supply blood to the head region, the arteries of the fourth arch become the **systemic arches,** which carry the blood to the dorsal aorta, and the arteries of the sixth arch become the **pulmo-cutaneous arches,** each of which divides into a **pulmonary artery** going to

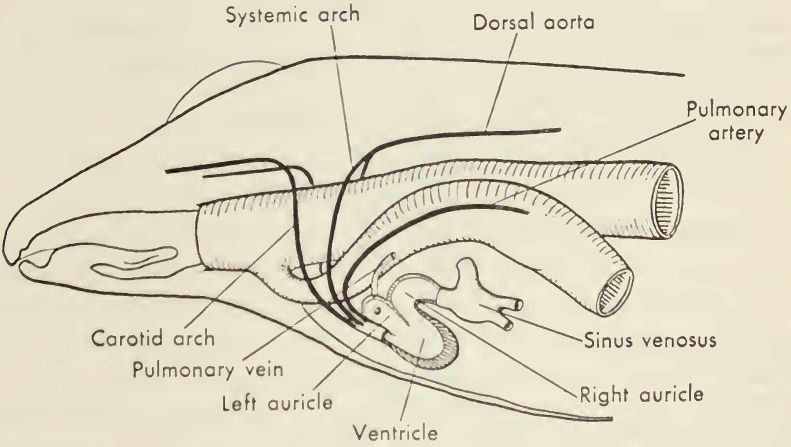

Fig. 31:7 Diagrammatic side view of the circulation in the anterior portion of a frog. The carotid arch is formed from the third aortic arch of the embryo, the systemic arch from the fourth aortic arch of the embryo, and the pulmonary arch from the sixth aortic arch of the embryo.

the corresponding lung and a **cutaneous artery** going to the skin along the side of the body (Fig. 31:7). It is thus seen that the circulatory system of the tadpole, which is adapted to breathing by means of gills, becomes modified in the frog and adapted to its method of breathing through its skin and lungs.

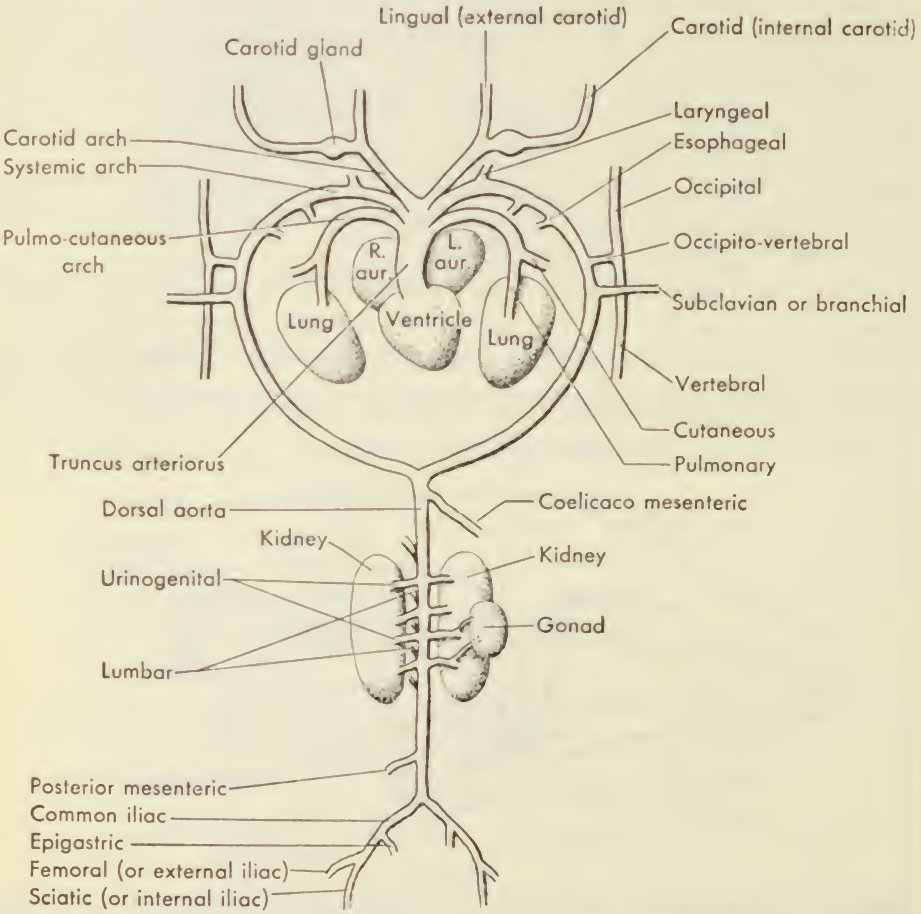

Fig. 31:8 Diagram of the arterial system of the frog, ventral view. Since the diagram shows a ventral view, vessels on the right side of the frog appear on the left side in the diagram and vice versa. R. aur., right auricle; L. aur., left auricle.

In the adult frog all the blood to the various organs of the body, with the exception of the lungs and a portion of the skin, goes through the carotid and systemic arches. These arteries with their branches and continuations form what is called the **systemic arterial system** (Fig. 31:8). Each of the **carotid arches**[1] divides, forming a **lingual artery**[2] and a

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[1] Called also **common carotid artery.**

[2] Called also **external carotid artery.**

carotid artery[1] which near its origin passes through a spongy network of blood vessels called the **carotid gland.** The lingual arteries carry blood to the ventral portion of the head and tongue, while the carotid arteries supply blood to the dorsal portion of the head, including the brain.

The two systemic arches unite dorsal to the pharynx to form the dorsal aorta. On their way around the pharynx after leaving the heart and before they unite, each of the systemic arches gives rise to several arteries. These are in succession a **laryngeal artery** to the larynx, **esophageal arteries** to the esophagus, an **occipito-vertebral artery** to the regions of the skull and vertebral column, and a large **subclavian artery** to the shoulder and forelimb. Near its point of origin the dorsal aorta gives rise to the **coeliaco-mesenteric artery.** This large artery supplies blood to most of the digestive organs in the body cavity. It soon divides into a **coeliac artery** and an **anterior mesenteric artery.** The coeliac artery divides to form an **hepatic artery** to the liver, a **gastric artery** to the stomach, and a **pancreatic artery** to the pancreas. The anterior mesenteric artery supplies blood to the spleen (an organ yet to be considered) and the small intestine. Returning to the dorsal aorta, as it courses along the dorsal body wall it gives off **urinogenital arteries** to the kidneys and the **gonads, lumbar arteries** to the body wall, and a **posterior mesenteric artery** to the large intestine. In the posterior part of the body cavity the dorsal aorta bifurcates, forming two **iliac arteries**[2] which supply blood to the hind legs. Each iliac artery sends an epigastric artery to the pelvic region and then divides, giving rise to a femoral artery[3] which goes to the muscles and skin of the thigh and a sciatic artery[4] which supplies the hind leg. Each of the pulmo-cutaneous arches divides to form a **pulmonary artery** to the corresponding lung and a **cutaneous artery** which runs to the skin of the corresponding side of the body. Everywhere in the body the finest branches of the arteries end in capillaries and from these capillaries the blood goes into veins which carry it back to the heart.

10. THE VENOUS SYSTEM OF THE FROG

In the lungs the blood from the pulmonary arteries passes into a network of fine capillaries which extends over the whole inner surface, separated from the air only by a thin lining of epithelial cells. From these capillaries the blood is carried directly to the left auricle of the heart in the pulmonary veins. The blood from all other parts of the body passes into the sinus venosus and from there to the right auricle.

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[1] Called also **internal carotid artery.**

[2] Called also **common iliac arteries.**

[3] Called also the **external iliac.**

[4] Called also the **internal iliac.**

The sinus venosus is a large, thin-walled, triangular structure, the base of the triangle being directed anteriorly, and the apex posteriorly

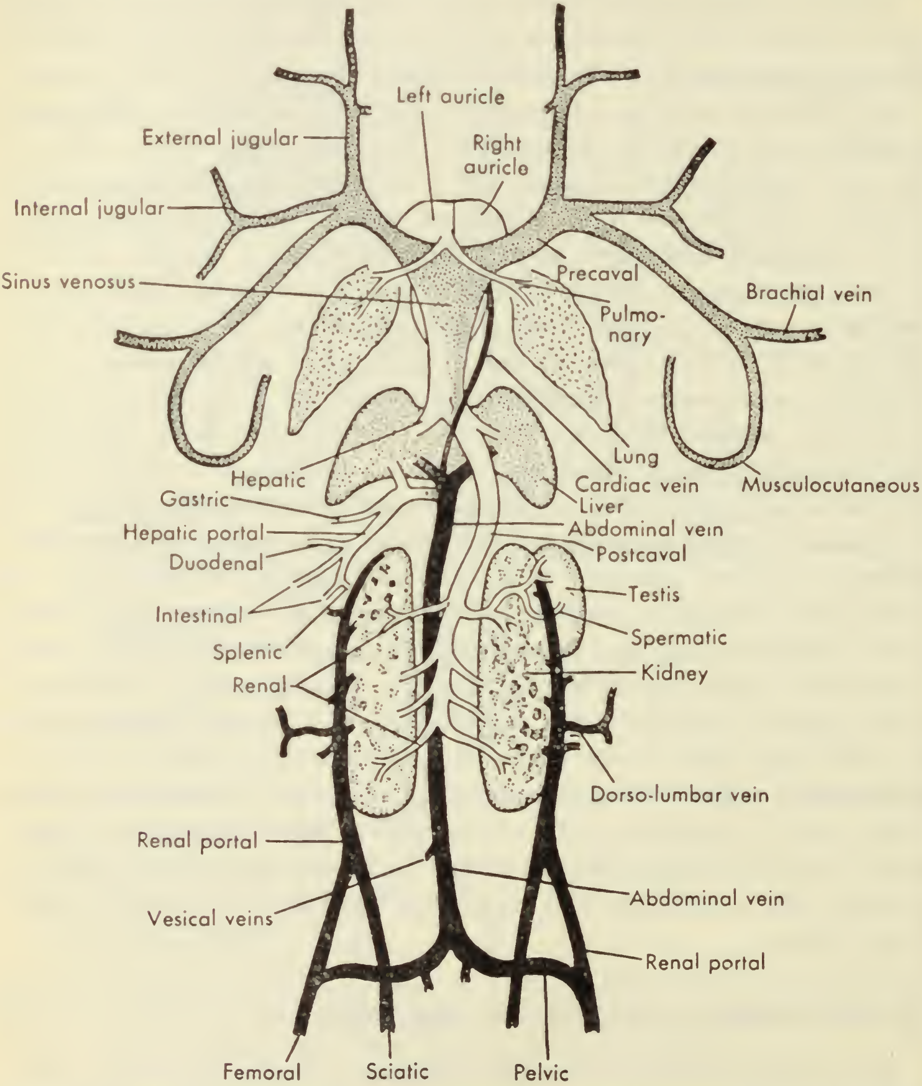

Fig. 31:9 Venous system of the frog seen from the dorsal side. From Holmes, *Biology of the Frog*, The Macmillan Company.

(Fig. 31:9). Three large veins enter at the three angles of the triangle; anteriorly on either side is a **precaval vein,**[1] posteriorly is the single **postcaval vein.**[2] Following up either of the precaval veins we find that it is formed by the union of three veins, an **external jugular vein** bringing blood from the head region, an **innominate vein** bringing blood from the head and shoulder, and a **subclavian vein.** The latter is formed by the union of a **musculocutaneous vein** from the skin and a **brachial vein** from the forelimb.

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[1] Called also **anterior vena cava.**

[2] Called also **posterior vena cava.**

In tracing the course of the blood from the posterior portions of the body and the viscera it will be best to follow it from the tissues and organs where the smaller veins take their origin. The blood from the hind legs is not returned directly to the heart but on its way must pass through either the kidneys or the liver and, on account of the alternate paths which the blood may take, the veins in this part of the body are somewhat complicated. Two main veins, the **femoral** and the **sciatic,** bring the blood from the hind legs, the sciatic from the posterior and the femoral from the anterior side. After entering the body cavity each femoral vein gives off a branch called a **pelvic vein** and continues under the name of the **renal portal vein.** The pelvic veins from opposite sides of the body unite to form a median ventral **abdominal vein** which carries blood to capillaries in the liver. Each renal portal vein before it enters the kidney is joined by the sciatic vein of the same side. In the kidneys the renal portal veins divide up into capillaries. Thus the blood returning in the femoral veins may go either to capillaries in the kidneys or through the abdominal vein to capillaries in the liver, while the blood which returns in the sciatic vein must go to capillaries in the kidney.

From the capillaries of the kidneys the blood, which includes blood from the posterior portions of the body, both from the renal portal and from the renal arteries, passes by a series of renal veins into the large **postcaval vein.** This vein passes along the dorsal side of the body cavity close to and parallel with the dorsal aorta, and enters the sinus venosus.

We have yet to consider how the blood returns to the heart from the digestive organs, blood which, it will be remembered, is laden with the products of digestion. This part of the circulation is called the **hepatic portal system** and consists of branches from the various parts of the digestive tract which join to form the **hepatic portal vein.** In the liver the hepatic portal vein divides up into a network of capillaries. The blood from the capillaries of the liver is collected into **hepatic veins** which join the postcaval vein near where it enters the sinus venosus.

11. THE HEART OF THE FROG

The pericardial cavity which contains the heart has already been referred to as a separate portion of the coelom. The heart (Fig. 31:10) lies near the ventral surface of the body but is protected from injury by the pectoral girdle. The **sinus venosus,** which is dorsal to the rest of the heart, opens into the right auricle by the **sinuauricular aperture.** This aperture is guarded by two flaps of tissue which project into the right auricle and act as a valve preventing the blood from backing up into the sinus venosus when the auricle contracts. The pulmonary veins open directly into the left auricle which is the smaller of the two auricles. The blood from the two auricles passes into the single ventricle through the **auriculoventricular aperture** which acts as a common opening for both auricles. Two large flaps of tissue, one on the dorsal and one on the ventral side of the aperture, form a valve which prevents the return of

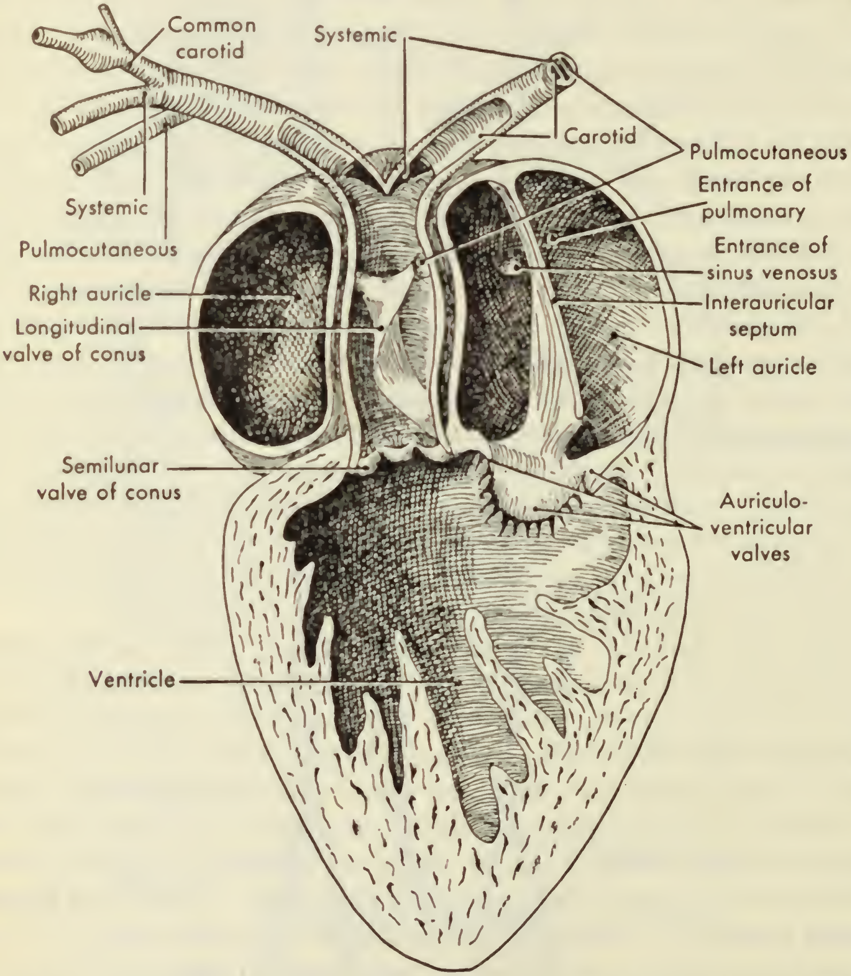

Fig. 31:10 A dissection of the heart of the frog from the ventral aspect. Drawn by B. B. Root from Hegner, *College Zoology*, The Macmillan Company.

the blood from the ventricle to the auricles. The thickness of the walls of the heart increases progressively from the sinus venosus to the ventricle, the latter being the most muscular part of the heart. From the ventricle the blood goes to the **conus arteriosus,** the opening into which is guarded by three semilunar flaps forming a valve. The conus arteriosus is continuous with the ventral aorta which gives rise to the aortic arches.

As already noted, with the development of lungs and pulmonary vessels the heart of the frog becomes partly divided, i.e., the auricle becomes divided into right and left auricles and the sinus venosus empties into the right auricle. With these changes the circulation of the blood of the frog comes to consist of two partially separated circuits each passing through the heart. One of these circuits takes the blood from the heart to the lungs and back to the heart and is called the **pulmonary circulation.** The other, called the **systemic circulation,** takes the blood to all the various organs of the body with the exception of the lungs and returns it to the heart. The separation between these two circulations is complete in the auricles, the blood from the lungs going to the left auricle while that from the rest of the body goes to the right auricle.

The two auricles contract simultaneously and when they do the blood is forced into the ventricle. In the ventricle the blood from the right and left auricles becomes somewhat mixed but not so much as it might otherwise be, because the walls of the ventricle are extended irregularly into its cavity giving it an almost spongy structure in the spaces of which the blood tends to remain. When the ventricle contracts the blood passes into the conus arteriosus. The first blood to enter is the blood from the right side of the ventricle. This blood came into the ventricle mostly from the right auricle, that is, from the sinus venosus and is nonaerated blood from the systemic circulation. The blood takes the path of least resistance and goes in the pulmonary arch to the skin and lungs. The next blood to enter the conus is that from the median portion of the ventricle and consists of partially mixed blood which goes into the systemic arches since they offer less resistance than the carotid arches. The carotid arches which go to the head region and the brain receive the blood from the left side of the ventricle which came there from the left auricle. This blood came to the left auricle from the lungs and is therefore aerated blood.[1] Thus by the division of the originally single auricle into right and left auricles the single circulation characteristic of the fish and the embryo tadpole is changed into two circulations, one of which, the pulmonary circulation, takes the blood received from the body and passes it to the lungs while the other, the systemic circulation, takes the aerated blood received by the heart from the lungs, distributes it to the body, and returns it to the heart.

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[1] The longitudinal valve in the conus arteriosus undoubtedly also plays a part in the separation of the two kinds of blood but its action is not clearly understood.

12. THE ARTERIAL SYSTEM OF MAN

Although the human embryo does not breathe by means of gills at any period in its life, at a certain stage in its development there appear five pairs of gill clefts, and six pairs of gill arches, similar to those of the dogfish and the tadpole (Fig. 31:11), excepting that in the human embryo the "clefts" do not normally open to the exterior but show as grooves on the sides of the head and neck and the inside of the pharynx. In the gill arches are aortic arches connecting the ventral aorta, which is a double vessel, with the dorsal aorta, which is also a double vessel.

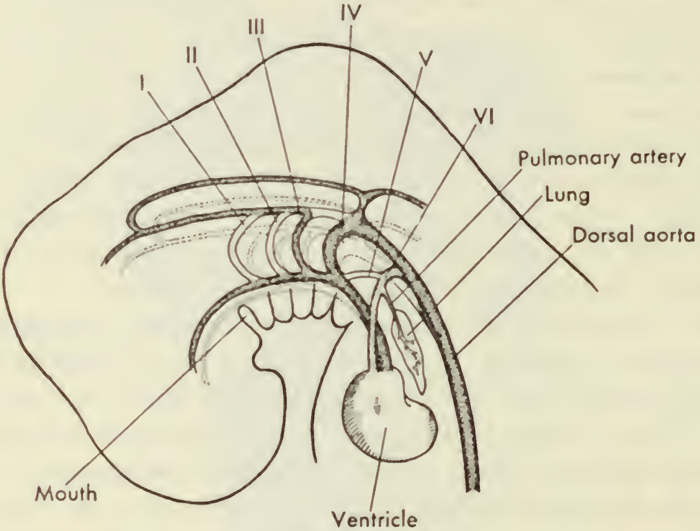

Fig. 31:11 Head of a human embryo, side view, showing the development of the arterial system. I, II, III, IV, V, VI, aortic arches. I, II, and V do not persist, while III forms the internal carotid arteries, IV forms a portion of the dorsal aorta, and VI forms the pulmonary arteries of the adult. Redrawn after Patterson, *Embryology*, by permission of the Oxford University Press.

After birth, in man and in mammals generally the function of pumping the blood through the lungs is taken over by the right side of the heart, while that of pumping the blood through the systemic circulation, which includes all the rest of the body, is carried out entirely by the left side of the heart. In consequence of this division of labor the heart, which in the embryo begins as a single tube, becomes completely divided into right and left halves.

In the course of development the blood vessels of the embryo noted above become modified into those of the human adult (Fig. 31:12). The **first two pairs of aortic arches** disappear. The **third pair of arches** with the portions of the dorsal aortae in front of them become the **internal carotid arteries** while the corresponding portions of the ventral aortae form the **external carotid arteries.** The portions of the ventral aortae between the third and fourth arches become the **common carotid arteries,** while the corresponding portions of the dorsal aortae disappear. Of the **fourth aortic arches,** which, it will be remembered, form in the frog the systemic arches, that on the right becomes the right **subclavian artery,** while that on the left persists as the aortic arch connecting the ventral and dorsal aortae, the left subclavian artery being developed independently of the gill arches. In the form which the arterial system finally takes the right common carotid and the right subclavian arteries do not arise separately from the aorta but as branches of a short **innominate artery** which connects them with the aorta. The right and left internal carotids supply blood to the brain and eye, the external carotids to the throat, tongue, and face. The subclavian arteries supply blood to the arms.

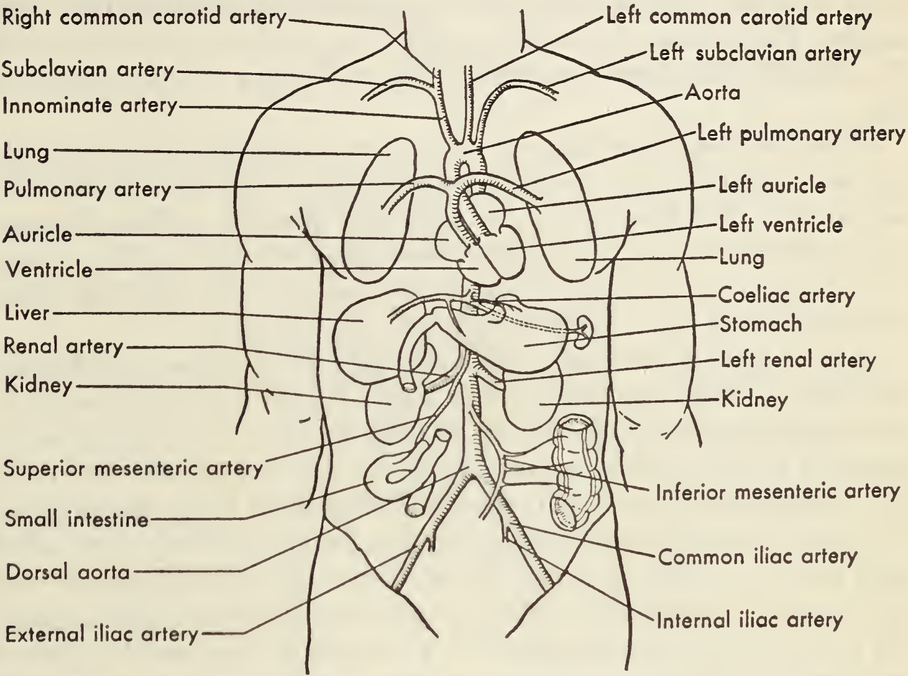

Fig. 31:12 A diagram of the main large arteries in the human arterial system. Since the diagram represents a ventral view, arteries on the right of the subject appear on the left in the diagram.

After entering the peritoneal cavity the dorsal aorta gives rise in succession to **coeliac, superior** [1] **mesenteric,** and **inferior mesenteric arteries.** The coeliac artery divides, giving rise to arteries which go to the stomach, spleen, and liver. The superior mesenteric artery goes to the small intestine and the ascending colon, while the inferior mesenteric artery goes to the descending colon, and the rectum. In the pelvic region the dorsal aorta divides to form right and left **common iliac arteries,** each of which divides again into an **external** and an **internal iliac artery.** The internal iliac artery goes to the viscera in the pelvis while the external iliac artery becomes the **femoral artery** which supplies the leg.

When the conus arteriosus of the embryo becomes divided into right and left halves the aorta becomes continuous with the left half and connected with the left ventricle. The **fifth pair of aortic arches** disappear in man as they do in the frog. The **sixth pair of aortic arches** become the pulmonary arteries and being continuous with the right half of the conus arteriosus are connected with the right ventricle.

In the course of this study of the arterial systems of the dogfish, frog, and man we have been able to trace how a circulatory system, which in the beginning was adapted to an aquatic existence and respiration by means of gills, has become gradually modified and adapted to the needs of a terrestrial existence and respiration by means of lungs. Not only can we trace this modification from the dogfish, through the frog, to the adult man but we are able also to see how the embryos of the frog and of man have systems of circulation closely resembling that of the dogfish, repeating as it were an ancestral condition. The study of the arterial systems of vertebrates provides one of the best examples of what is known as the **theory of recapitulation** which states that an individual in its development passes through a series of stages which correspond to the adult stages of species from which it was descended.

13. THE VENOUS SYSTEM OF MAN

We will not attempt to trace the development of the venous system in man but merely describe it in the adult (Fig. 31:13). A single large vein called the **superior vena cava** or **precava** brings the blood from the upper part of the body to the right auricle. This vein is formed by the union of two innominate veins, one from each side of the body. Each innominate vein is formed by the union of an internal jugular, an external jugular, and a subclavian vein. The **internal jugular** brings blood from the brain, the **external jugular** from the face, and the **subclavian** from the arm. From the abdomen and the lower part of the body the blood goes to the heart in the **inferior vena cava** or **postcava.** Just below the diaphragm it receives the **hepatic veins** from the liver. In the peritoneal cavity it receives the **renal veins** from the kidney and veins from the abdominal wall. Near the pelvis it takes its origin from the union of a right and a left common iliac vein. The **common iliac veins** are each formed by the union of an external and an internal iliac vein. The **internal iliac veins** receive blood from the viscera of the pelvis, while the **external iliac veins** are the continuations of the **femoral veins** from the legs. In man all the blood from the legs returns directly to the heart and blood comes to the kidneys only by way of the renal arteries. It will be remembered that in the frog blood comes to the kidneys not only in the renal arteries but also in the renal portal veins, vessels which are not present in the circulatory system of man.

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[1] On account of man's erect posture the terms "superior" and "inferior" are commonly used in human anatomy in place of the terms "anterior" and "posterior" used to express the same anatomical relations in the frog and other animals.

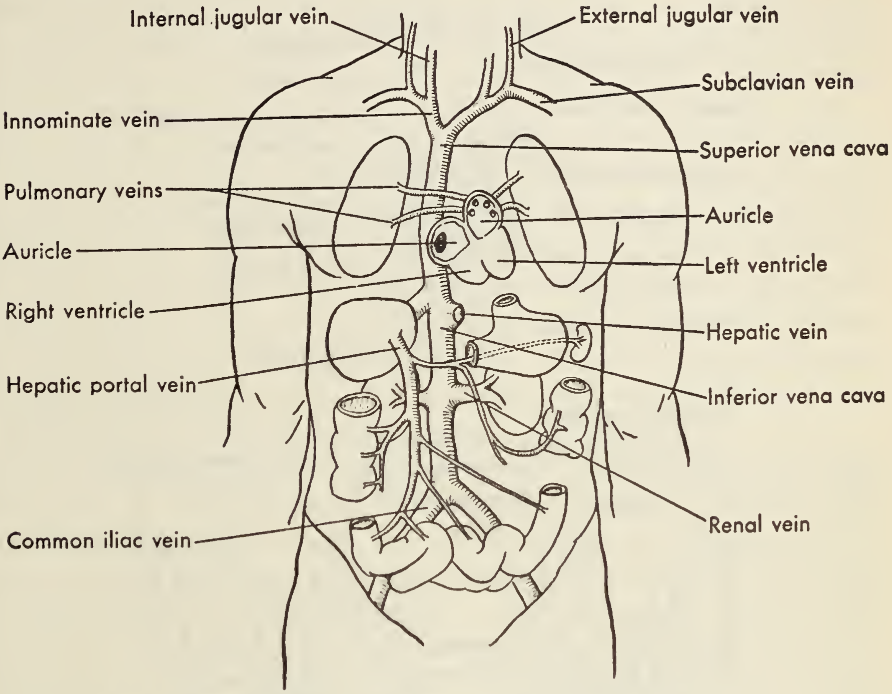

Fig. 31:13 A diagram of the human venous system, ventral view.

The **hepatic portal system** of veins in man is similar to that in the frog. Blood is collected from the stomach, the small intestine, and the large intestine and carried to capillaries in the liver. From the liver the blood is carried in the **hepatic veins** to the inferior vena cava as already mentioned.

14. THE HUMAN HEART

In the human heart (Fig. 31:14) the sinus venosus, which in the frog opens into the **right auricle,** becomes united with the right auricle so that the veins bringing the blood from the body in the systemic circulation appear to open directly into that auricle. In the right auricle the sinus venosus is represented by an important structure called the **sinu-auricular node** which will be referred to later. The right auricle communicates with the **right ventricle,** the opening being guarded by a

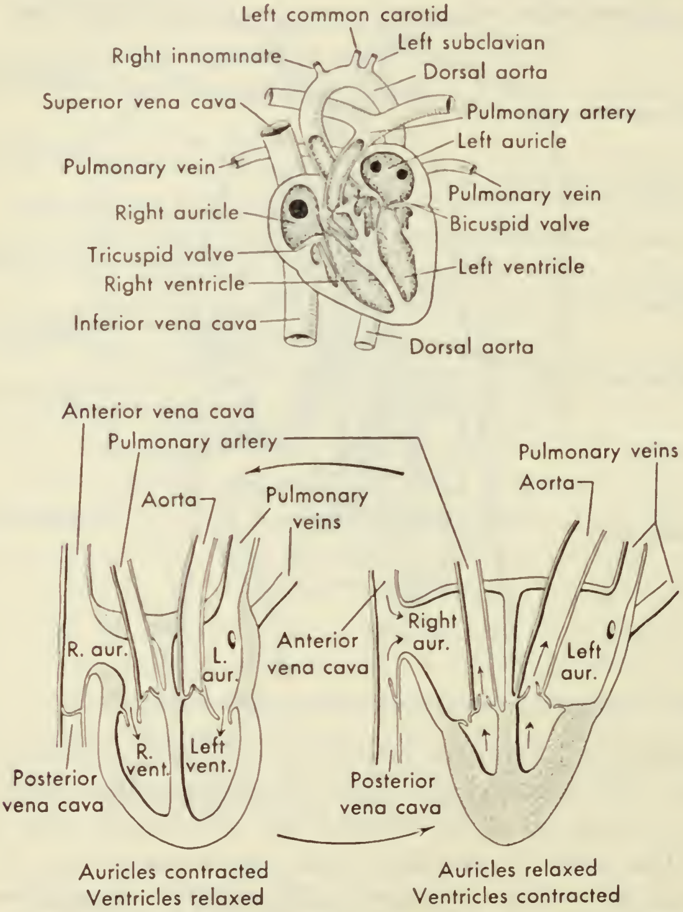

Fig. 31:14 The mammalian heart. Above dissected to show the interior. Redrawn after Adams, *An Introduction to the Vertebrates*, by permission of John Wiley & Sons. Below diagrams showing the heart in action. Shaded areas indicate contracted muscles.

valve consisting of three flaps and hence called the **tricuspid valve.** From the right ventricle the blood goes to the pulmonary artery, the entrance to which is guarded by **semilunar valves.** In the pulmonary arteries the blood is taken to the lungs.

The **pulmonary veins** open into the left auricle, as in the case of the frog. The left auricle opens into the **left ventricle** by an opening guarded by a valve composed of two flaps and therefore called the **bicuspid valve.** In consequence of the greater force required to send the blood through the systemic circulation the left ventricle is larger and more muscular than the right. The aorta arises from the left ventricle and contains **semilunar valves** near its point of origin.

For a clear understanding of the circulation of the blood in man it is important to understand that the heart consists of two complete and separate pumps. That of the right side may be called the **pulmonary pump,** that of the left side the **systemic pump.** In forcing the blood through its particular part of the general circulation each pump goes through a cycle in which the auricle and ventricle are alternately relaxed and contracted. The auricles and ventricles of opposite sides relax and contract simultaneously, but apart from this each side of the heart may be considered as a separate mechanism.

We will consider first the pulmonary pump which consists of the right auricle and the right ventricle. When the right auricle is relaxed, blood flows into it from the systemic circulation through the superior and inferior venae cavae. While this is occurring the tricuspid valve guarding the opening to the ventricle is closed so that the auricle becomes filled with blood. When this occurs the muscles of the auricle begin to contract and since at this time the muscles of the ventricle are relaxed the tricuspid valve opens and blood flows from the auricle into the ventricle. Now follows the contraction of the right ventricle and the closing of the tricuspid valve, due to the fluid pressure developed there being greater than in the auricle which begins to relax. The mounting pressure in the ventricle causes the semilunar valves in the pulmonary artery to open. The muscles of the ventricle continue to contract, and the blood is driven through the pulmonary arteries into and through the capillaries of the lungs. From the lungs the blood is carried in the pulmonary veins to the left auricle.

The systemic pump consists of the left auricle and the left ventricle. It drives the blood through all the organs and tissues of the body except the lungs. When the left auricle is relaxed the blood from the pulmonary veins flows into it; and since the bicuspid valve is closed it becomes filled. The left auricle now contracts and, as the fluid pressure within it increases and the muscles of the ventricle remain relaxed, the bicuspid valve opens, allowing the blood to flow into and fill the left ventricle. When filled the left ventricle begins to contract and, as the pressure within it gradually increases, first the bicuspid valves are closed and then the semilunar valves of the aorta open. As the muscles of the ventricle continue to contract the blood is driven through the aorta and its various branches, and sufficient pressure is maintained to force it through the capillaries of the systemic circulation. From these capillaries the blood passes into the veins. It eventually reaches the anterior or posterior vena cava and is delivered to the right auricle to be pumped to the lungs and go through another cycle.

While the blood passes through the two separate circulations, the pulmonary and the systemic in sequence, the two pumps represented by the right and left sides of the heart act simultaneously so that the right and left auricles contract together and the right and left ventricles contract together. In a normal, healthy, resting adult the heart beats, i.e., the auricles and ventricles contract, sixty-five to eighty times per minute or a little over once per second depending on age and other constitutional factors. It does this with a regularity which rivals that of the second hand of a watch.[1] The heart is not only remarkably regular in its beating; it beats continuously from before birth to death. One may well ask by what mechanism this is achieved.

It is not surprising to learn that an organ as important for the body as the heart is controlled not in one but in a number of different ways. A frog's heart, when taken out of the body and completely disconnected from the brain and spinal cord, will continue to beat regularly. It is comparatively easy to show experimentally that in the frog heart the "pace" is set by the sinus venosus, i.e., that the rate of beat of the other parts of the heart (auricle and ventricle) depends on the rate at which the sinus venosus goes through its cycle. In man the pace is set by the sinuauricular node. However, in the intact animal the heart is not free from nervous control. Stimulation of the tenth cranial or vagus nerve causes a slowing down of the heartbeat and when the stimulus is sufficiently intense the heart is stopped. This action of the vagus is referred to as "inhibition of the heart." Other nerves when stimulated accelerate the heart. These nerves affect chiefly the sinus venosus in the frog and the sinuauricular node in man. Further experiments have shown that there exist on each side of the hind brain (medulla) centers which control the heart. One pair of these, called the **cardioinhibitor centers,** inhibit the heart through the vagus as already noted. The other pair, called the **cardioaccelerator centers,** accelerate the heart through the sympathetic system.

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[1] It is interesting to note in this connection that Galileo in experiments which are often regarded as marking the starting point of modern science, timed his falling bodies by counting his pulse.

The pulse, which can be felt in various parts of the body such as the neck, ankle, or wrist is due to the wave of blood pressure which passes along the systemic arteries each time the left ventricle contracts. It occurs slightly after the contraction of the ventricle but of course has the same rhythm. The term **blood pressure** is usually applied to the fluid pressure in a blood vessel. It varies along the length of an artery, being greatest nearest to the heart and gradually falling off in the capillaries and veins. It is usually determined by the physician for the brachial artery just above the elbow where the pressure corresponding to the peak of the ventricular contraction is normally equivalent to 120 to 140 millimeters of mercury. At the beginning of the capillaries the blood pressure is still relatively high, being equivalent to 40 to 60 millimeters of mercury. At the venous ends of the capillaries it is much lower, being equivalent to only 15 millimeters.

This difference in blood pressure at the beginning and ends of the capillaries is of great importance in the transfer of materials from the capillaries to the tissues and vice versa. At the beginning of the capillaries the blood pressure is greater than the osmotic pressure of the blood. Hence the plasma and the diffusible materials which it contains, including oxygen, salts, and sugar, diffuse out into the tissue spaces and become part of the lymph. At the venous end the blood pressure is less than the osmotic pressure of the blood in the capillaries, and in consequence tissue fluids, containing carbon dioxide and waste products, diffuse into the capillaries.

15. THE SPLEEN

The spleen in the frog is a small, spherical, dark-colored body in the mesentery not far from the stomach. In man it is an irregularly shaped body about 3 or 4 inches in diameter located behind the stomach. It acts as a reservoir in which blood may be stored to be released into the circulation when needed. It is under control of the autonomic nervous system (Chap. 32). When blood is lost by profuse bleeding the smooth muscles surrounding the spleen contract, reducing its size and forcing blood into the splenic veins. This also occurs in times of emergency, such as those which cause adrenalin to be poured into the blood (see Chap. 34).

16. THE LYMPHATIC SYSTEM

In most cases the cells of the tissues of the body are more or less loosel fitted together so that small irregular spaces occur between them. Thes spaces are filled with a fluid called **lymph.** The liquid part of the lymp resembles the plasma of the blood from which it arises by diffusion an filtration through the walls of the capillaries. It usually contains less protein substance than the blood and may, as in the case of the lacteals, contain considerable quantities of fat in the form of small globules. The leucocytes of the blood frequently wander through the walls of the capillaries and are found in the lymph.

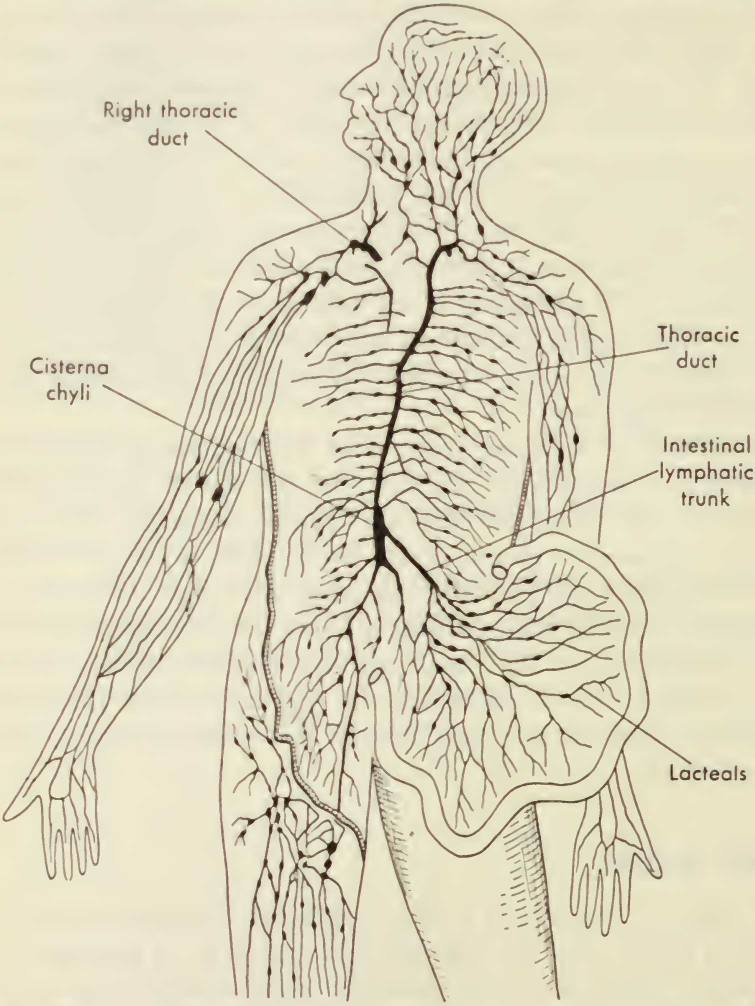

Fig. 31:15 Diagram of the human lymphatic system, partly adapted from Zoethout and Tuttle, *Textbook of Physiology*, The C. V. Mosby Company.

In the frog there are no regular lymphatic vessels like the vessels which carry the blood. The lymph, however, collects in **lymph spaces** in certain parts of the body, particularly under the skin and between the vertebral column and the body cavity. From these spaces the lymph is pumped by lymph hearts into the venous system. Two of these lymph hearts occur, one on either side of the third vertebra, and pump lymph into the vertebral veins which are branches of the internal jugulars. The other two lie on either side of the tip of the urostyle and pump lymph into branches of the transverse iliac veins which provide cross connections between the sciatic and femoral veins. If it were not for the action of the lymph hearts, the frog's body would become waterlogged. The lymph hearts pump the excess fluid from the tissues into the blood stream and from there it is excreted by the kidneys.

In man there are definite lymph capillaries which join to form larger lymph vessels called **lymphatics** (Fig. 31:15). These latter lead into two main vessels. One, called the **thoracic duct,** runs along the dorsal wall of the upper part of the abdomen and thorax and empties into the left innominate vein; the other, called the **right thoracic duct,** is much smaller and joins the right innominate vein. There are no lymph hearts in man, the lymph being moved largely by the general muscular movements of the body.

In man and the frog the fluid which fills the cavities in the body is also part of the lymph, although in these cavities it receives special names. These lymph-filled cavities include the pleural cavities, the pericardial cavity, the peritoneal cavity, and the synovial cavities of the joints.

17. THE INTERNAL MEDIUM

The lymph in which most of the cells of the body are bathed forms their environment, just as the pond water forms the environment of an amoeba. This environment of the cells of the body, referred to in an earlier chapter as the internal medium, is determined largely by the composition of the blood and its circulation through the body. Any change in the blood immediately leads to a change in the internal medium and any change in the flow of the blood through the body changes the rate of diffusion between the capillaries and the internal medium. Hence the importance of the circulation in maintaining the constancy of the internal medium. The proper composition and the constancy of the internal medium are essential for the proper functioning of the different organs of the body.

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11. The heart of the frog 603
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13. The venous system of man 608
14. The human heart 610
15. The spleen 613
16. The lymphatic system 614
17. The internal medium 615

Questions

1. Describe the blood of man and compare it with that of the frog.
2. Discuss the functions of the blood.
3. How would you distinguish between an artery, vein, and a capillary (*a*) structurally and (*b*) functionally?
4. Trace the course of the circulation in a simple vertebrate such as the dogfish.
5. Trace a path which might be taken by a blood corpuscle in a frog in going (*a*) from the stomach to a lung, (*b*) from a hind leg to the heart, (*c*) from a lung to the head.
6. Describe the two paths which a frog's blood corpuscle may take in returning from the hind leg to the heart.
7. Trace a path which a human blood corpuscle might take from the time it leaves a capillary in the lung until it returns to a capillary there. (Note that there is a double circulation in man and that the corpuscle must pass through the heart twice.)
8. What advantages has the human circulatory system over that of the frog?
9. Where is the blood richest in oxygen? In carbon dioxide? Where is the blood richest in urea? Where is it poorest in it?
10. Why are the terms "pure" and "impure" blood unsatisfactory?
11. How does lymph differ from blood?
12. Where does the lymph enter the venous system in the frog? In man?
13. Of what advantage is it to the body to have a constant internal medium?

Suggestions for Further Reading

Amberson, William R., and Dietrich C. Smith, *Outline of Physiology*, F. S. Crofts & Co., New York, 1939, Chaps. XVI and XVII.

Best, Charles H., and Norman B. Taylor, *The Living Body, A Text in Human Physiology*, Henry Holt and Company, Inc., New York, 1938, Chap. III.

Kimber, Diana C., Carolyn E. Gray and Caroline E. Stackpole, *Textbook of Anatomy and Physiology*, The Macmillan Company, New York, 1935, Chaps. XI–XV.

CHAPTER 32

The Nervous System

The vertebrate **nervous system** is made up of three main parts: th **central nervous system,** which consists of the brain and spinal cord; th **peripheral nervous system,** consisting of the nerves to the various organ and tissues; and the **autonomic system,** which includes ganglia or group of nerve cells located in different parts of the body exercising control o the viscera and blood vessels.

1. THE NERVE CELL OR NEURON

The unit of structure of the nervous system is the nerve cell or **neuron.** Just as in the digestive system the processes of secretion, absorption, and assimilation are carried on by the individual cells, so in the nervous system the impulses which activate and control the organs, tissues, and cells of the body are originated and are distributed by cells. The most conspicuous feature of a nerve cell is the prolongation of its protoplasm into long, fine processes (Fig. 32:1). So long and so fine are these processes that it would be practically impossible for the eye to see all of such a nerve cell at one time, even if the cell could be completely isolated from the surrounding tissues. A magnification which makes the cell with its processes visible would make the processes of such a length that they disappeared in the distance. The cell body of the neuron shown, i.e., the cell minus its processes, is found in the ventral (in man the anterior) part of the spinal cord. It contains a nucleus with a well-defined nucleolus.

Two kinds of protoplasmic processes go out from the cell body. One kind, called **dendrites,** are relatively thicker, are granular as they leave the cell, and extend in all directions, branching in a rootlike fashion. The other kind is represented by a single long process called the **axon,** which arises from a cone-shaped projection of the cell and is relatively hinner and longer than the dendrites. If the neuron illustrated happened o be one of those which supply fibers to the muscles of the foot or hand he length of the axon might be a meter or more. The cell body has een drawn at a magnification of four hundred. Thus if the axon were

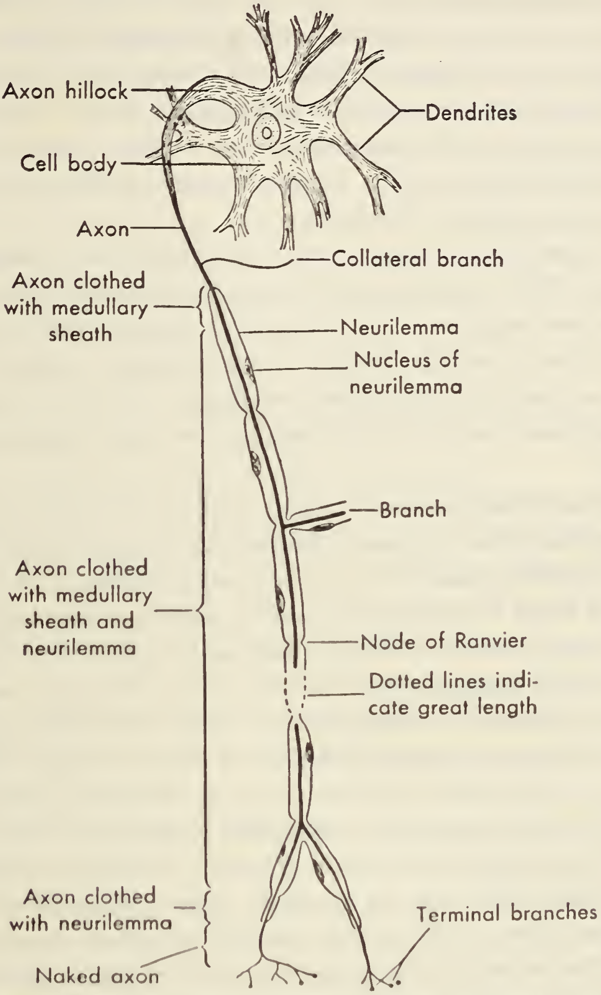
Axon hillock
Dendrites
Cell body
Axon
Collateral branch
Axon clothed with medullary sheath
Neurilemma
Nucleus of neurilemma
Branch
Axon clothed with medullary sheath and neurilemma
Node of Ranvier
Dotted lines indicate great length
Axon clothed with neurilemma
Terminal branches
Naked axon

Fig. 32:1 A neuron. The medullary sheath is here indicated as a thick, clear area surrounding the axon. The cells of the neurilemma are exceedingly thin and except for their nuclei are indicated by lines surrounding the medullary sheaths. From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, The Macmillan Company.

drawn to the same scale, it would extend for 400 meters or about ¼ mile. The axon may give off a few **collateral branches** before reaching the muscle. In the muscle the axon divides to form branches which go to the individual muscle cells.

For most of its length the axon is enclosed in two cylindrical sheaths.

The inner of these is called the **medullary sheath** and is composed of a fatty substance. The outer is called the **neurilemma** and consists of thin, elongated cells wrapped round the medullary sheath. At fairly frequent intervals, usually of less than 1 millimeter, the medullary sheath is interrupted at the **nodes of Ranvier.** At these nodes the neurilemma seems to come directly in contact with the axon. The nuclei of the cells of the neurilemma occur between the nodes of Ranvier. It is believed that the function of the medullary sheath is to keep the nerve impulse traveling within the axon, in other words to act as an insulator, while the function of the neurilemma seems to be to pass nourishment to the protoplasm of the axon at the nodes of Ranvier.

The above description applies more particularly to a **motor neuron,** i.e., a neuron which conducts nerve impulses from the central nervous system to a motor organ such as a muscle or a gland. In the case of such a neuron the axon is usually long for it extends from the cell body in the spinal cord or brain to the muscle or gland, while the dendrites are numerous and short and contained within the gray matter of the spinal cord or brain.

In **sensory neurons** there is usually a single long dendrite which brings the nerve impulse from the part stimulated, e.g., skin. The cell body is usually in a ganglion outside the spinal cord or brain. The axon may be comparatively short extending from the ganglion to the brain or spinal cord where it may break up into numerous branches. The sensory neurons of the dorsal ganglia are peculiar in that the axon and dendrite appear to be branches of a single process of the cell body (Fig. 32:2).

The actual ends of the nerve processes or nerve endings differ according to the part of the body in which they occur. In most cases the dendrite or axon splits up into many fine **terminal branches.** The neurilemma and the medullary sheath are absent from the terminal branches. In the brain and spinal cord and in nervous tissue generally the terminal branches of the axon of one neuron usually interlock with the terminal branches of the dendrites of other neurons. Sensory nerve processes going to the skin usually end in terminal branches which pass between the cells of the epidermis. The nerve endings in the special sense organs will be described later when considering these organs. The axons which go to the voluntary muscles end in nodular enlargements which are applied to the muscles.

The white glistening strands seen in dissections and called nerves are made up of bundles of nerve fibers, each fiber consisting of a nerve process, axon or dendrite, and its accompanying sheaths. Such nerves do not contain nerve cells. The nerve cells from which the fibers arise are ocated chiefly in gray matter of the brain and spinal cord, in sympathetic ganglia, and in the sense organs.

2. THE NERVE IMPULSE

The term **nerve impulse** is applied to the change of state which passes long the nerve fiber when it transmits a stimulus from one part of the ody to another. Usually nerve impulses travel to the cell body in the endrites and away from the cell in the axon, and it appears that in most ases a nerve impulse can pass through a nerve cell and its processes in nly one direction. Of the actual nature of the nerve impulse we know ttle. The rate at which it travels along nerve fibers is less in cold-blooded nimals like the frog than in warm-blooded animals like man. In the rog's sciatic nerve at room temperature the rate is between 24 and 38 neters per second, while in man it may be as much as 125 meters per econd. The rate varies in different animals, in different nerves in the ame animal, and in the same nerve under different conditions. In the rog it can be shown to vary with the temperature.

Many features point to the nervous impulse being the passage along he nerve of a chemical change accompanied by an electrical charge. It s certainly not simply an electric current passing through the nerve nd it is also certainly not a mechanical force such as a tension on the erve. That the propagation of the nervous impulse requires energy is hown by the fact that nerves take in oxygen, give off carbon dioxide, nd become heated when the impulse passes. However, the amount of nergy required for nervous activity is relatively much less than for the ther activities of the body.

Usually more than a single neuron is involved in any nervous action nd the nervous impulse must pass from one to the other. This passage f the nervous impulse usually occurs from the branches of the axon of ne cell to the dendrites of the other cell. The passage of the impulse s believed to be made possible by the intimate relation of the two processes and to occur only under certain physiological conditions. The term **ynapse** has been applied to this intimate relationship between two nerve rocesses. It has been found that in a synapse the nerve impulse can pass n only one direction and that the direction depends upon the synapse. The synapse has been shown to be the seat of fatigue in nervous activity.

3. THE SPINAL CORD

We begin the study of the central nervous system with the spinal cord ecause on the whole its structure is less complex than that of the brain and shows us the general plan of structure of the central nervous system The spinal cord lies in the neural canal protected from external pressure by the neural arches and centra of the vertebrae. In the neural canal, which it does not fill, the spinal cord is surrounded by three connective tissue membranes called the **meninges.** The outermost of these, called the **dura mater,** is hard and resistant. In the head it forms the lining of the cranium. In the spinal cord it is loosely attached to the periosteum

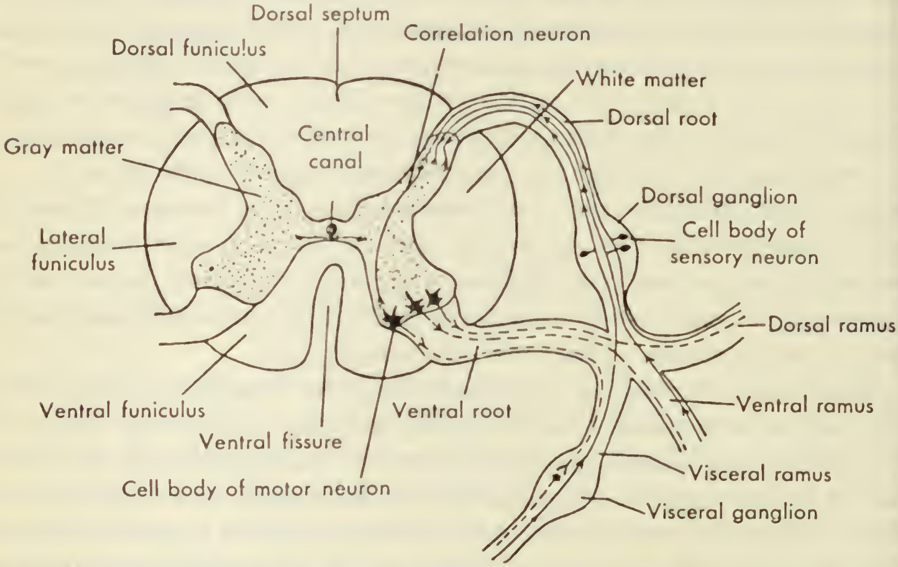

Fig. 32:2 A diagram of a cross section of the spinal cord with the dorsal and ventral roots of the spinal nerves. After Adams, *An Introduction to the Vertebrates*, by permission of John Wiley & Sons, Inc.

of the neural canal. Within the dura mater is a delicate membrane called the **arachnoid** (Gr. spiderlike). The innermost of the three membranes is the **pia mater** which is closely applied to the brain and spinal cord and contains blood vessels. Between the arachnoid and the pia mater is the **subarachnoid space** containing the **cerebrospinal fluid.**

The spinal cord is cylindrical in shape. In the frog it is somewhat flattened dorsoventrally, but in man it is almost circular in cross section. A fine line running along the dorsal side indicates where the **dorsal septum** comes to the surface and a groove extending along the ventral surface marks the entrance of the **ventral fissure** into the cord. The spinal cord extends from the foramen magnum where it is continuous with the brain to about the seventh vertebra in the frog and the second lumbar vertebra in man, where in each case it tapers into a fine nonnervous thread called the **filum terminale.** The **spinal nerves** leave the neural canal between the neural arches, but since the spinal cord is horter than the vertebral column and there are as many nerves as there are spaces between the vertebrae the more posterior nerves run posteriorly for some distance in the neural canal.

A **cross section of the spinal cord** shows us its internal structure and the cells of which it is composed (Fig. 32:2). In the center surrounded by a layer of epithelial cells is the **central canal** which extends the entire length of the cord and is continuous with the cavities of the brain. On the dorsal side the **dorsal septum** appears as a fine line while on the ventral side the **ventral fissure** extends inward toward the central canal. Surrounding the central canal and extending outward on either side dorsally and ventrally so as to give in the section the appearance of the letter H, is the **gray matter.** In this form the gray matter extends throughout the length of the spinal cord. The two dorsal portions, corresponding to the top part of the letter H in the section are called the **dorsal columns.** The two ventral portions are called the **ventral columns.** The middle portion which corresponds to the bar of the H and contains the central canal projects slightly on either side, forming **lateral columns.** The gray matter contains most of the cell bodies of the neurons of the spinal cord.

Outside the gray matter and occupying the rest of the section is the **white matter.** This part of the spinal cord consists mostly of nerve fibers, the medullary sheaths of which make it white. The fibers run lengthwise in the spinal cord and give off branches to the spinal nerves. Like the gray matter the white matter also is divided into portions which in this case are called **funiculi.** On either side of the dorsal septum is a **dorsal funiculus.** Between the dorsal and ventral columns of the gray matter on either side of the cord is a **lateral funiculus,** while on either side of the ventral fissure and between it and the ventral column of the gray matter is a **ventral funiculus.**

4. THE SPINAL NERVES

From the spinal cord arise the spinal nerves, which come off in pairs, one from each side of the cord. Like the vertebrae they are arranged metamerically which points clearly to a primitive metamerism of the vertebrate body. Each nerve arises by a dorsal and a ventral root. The nerve fibers of the dorsal root can be traced to the dorsal column of the gray matter in the spinal cord, while those of the ventral root can be traced to the ventral column of gray matter.

The cell bodies from which arise the nerve fibers of the **ventral root** are located in the ventral column of the gray matter, and the whole neuron has a structure similar to that of the neuron described at the beginning of this chapter. The axon runs out in the nerve and the dendrites ramify in the gray matter of the ventral column.

The cell bodies which give rise to the fibers running in the **dorsal root** of a spinal nerve are located not in the spinal cord but in an enlargement on the course of the nerve called the **dorsal ganglion.** From the cells in the dorsal ganglion processes go along the dorsal root into the gray matter of the dorsal column and in the opposite direction out along the nerve. Just beyond the dorsal ganglion and not far from the spinal cord the dorsal and ventral roots combine to form the nerve.

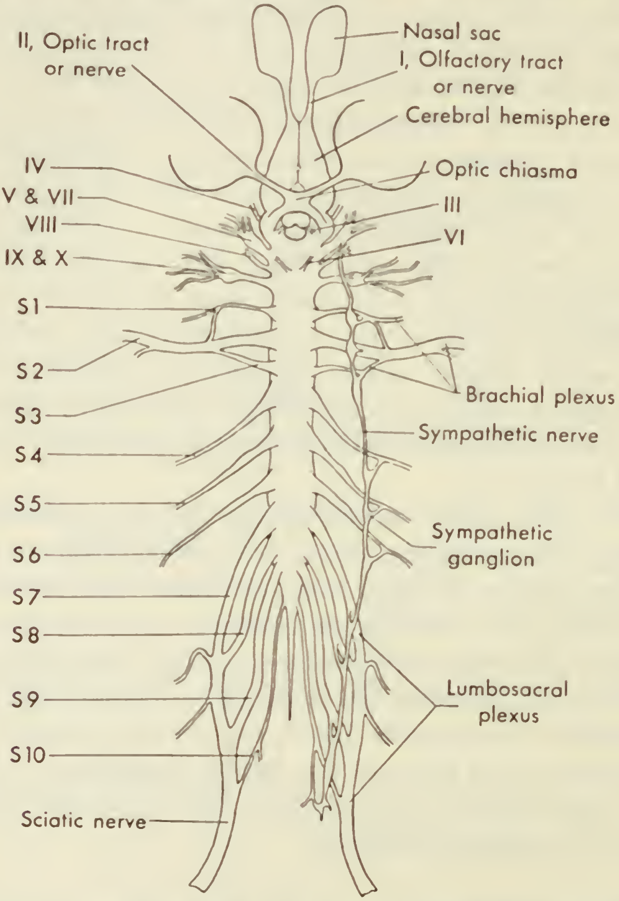

Fig. 32:3 The frog. A ventral view of the central nervous system, the origins of the cranial and spinal nerves, and the sympathetic system of one side. I–X, the ten cranial nerves; S1–S10, the ten spinal nerves.

The nerve fibers running in the dorsal root are found to be **sensory,** i.e., they carry nerve impulses to the spinal cord. For this reason they are called **afferent fibers** (L. *affero,* to carry to). The fibers running in the entral root are found to be **motor,** i.e., they carry nerve impulses from he spinal cord to muscles, glands, or other organs which respond by ontraction, secretion, or other special activity. They are called **efferent** **ibers** (L. *effero*, to carry from).

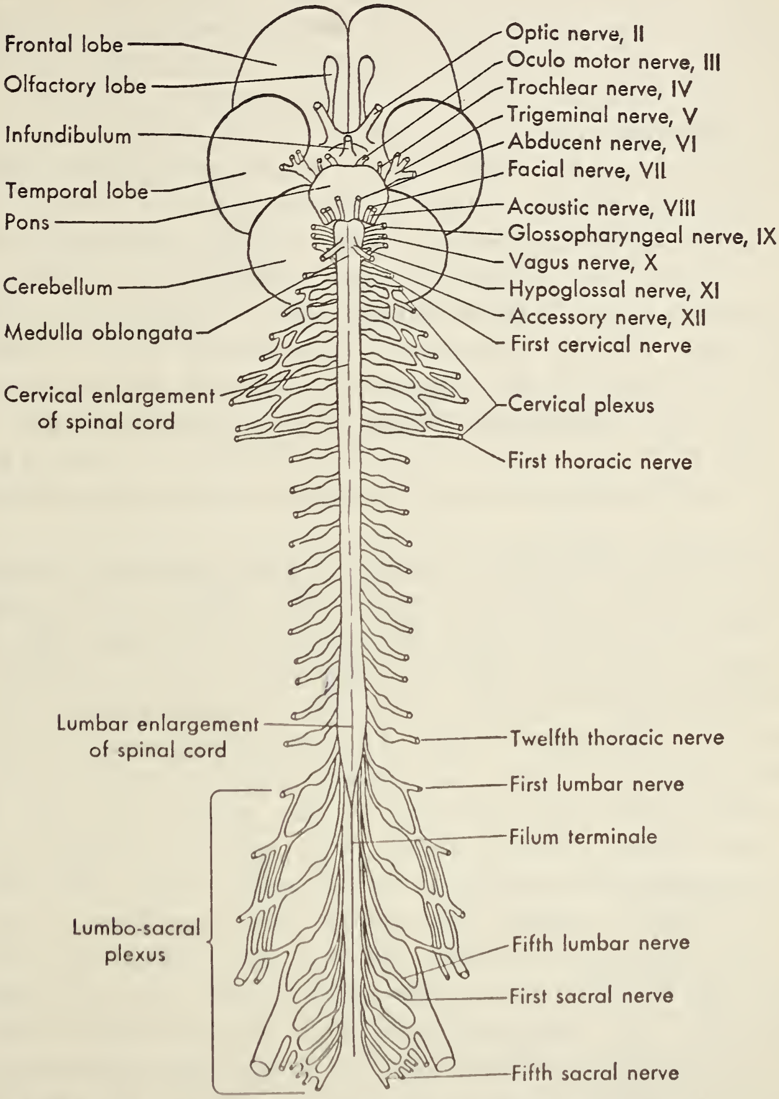

Fig. 32:4 Man. A ventral view of the central nervous system and the origins of the cranial and spinal nerves and the nerve plexuses. The term "cervical plexus" is used to include the cervical plexus proper, composed of the first four cervical nerves and the brachial plexus which includes the last four cervical nerves and the first thoracic nerve; the term "lumbo-sacral plexus" is used to include the lumbar plexus, composed of the first four lumbar nerves, and the sacral plexus which includes the fifth lumbar, the sacral, and the coccygeal nerves. The sympathetic system is not shown.

After its formation from dorsal and ventral roots a spinal nerve divide into three branches, a dorsal ramus (or branch), a ventral ramus, and visceral ramus, each of which contains both sensory and motor fiber (Fig. 32:2). The **dorsal ramus** goes to the skin and muscles of the dorsa side of the body, including the dorsal sides of the limbs; the **ventra ramus** goes to the ventral side of the body including the ventral side of the limbs; while the **visceral ramus** goes to the dorsal wall of the coelom where it connects with a visceral sympathetic ganglion.

In the **frog** there are ten pairs of spinal nerves, the first nine of which emerge from the neural canal posterior to the corresponding vertebra while the tenth emerges through a small opening or foramen in the urostyle (Fig. 32:3). The dorsal ganglia occur just as the nerves emerge from the neural canal. Usually the first three spinal nerves take part in the formation of the **brachial plexus,** which innervates the forelimb and shoulder. The next three nerves are small and go to the skin and muscles of the wall of the abdomen. The seventh, eighth, and ninth nerves form the **lumbosacral plexus** which innervates the hind limb The tenth nerve joins with a branch of the ninth to form a plexus which innervates the viscera in the posterior portion of the abdomina cavity.

In man (Fig. 32:4) thirty-one pairs of spinal nerves are recognized which are divided as follows: cervical, eight, thoracic, twelve, lumbar five, sacral, five, coccygeal, one. The reason for there being eight in the neck region is because the nerves are considered to come out behind their corresponding vertebrae except in the case of the first which comes out between the cranium and the atlas. There are formed cervical, brachial, lumbar, and sacral plexuses. The cervical plexus is formed by the first four cervical nerves and innervates the skin of the back of the head, neck, and shoulder, and the muscles of the neck and diaphragm, and sends communicating branches to the autonomic system. The brachial plexus is formed by the last four cervical nerves and the first thoracic nerve and innervates the thorax and arm. The cervical and brachial plexuses are connected and are sometimes together called the **cervical plexus.** The lumbar plexus is formed by the first four lumbar nerves. It innervates the buttock and the thigh. The sacral plexus is formed by part of the fourth lumbar nerve, the fifth lumbar, and the first three sacral nerves. It innervates the lower limb. The lumbar and sacral plexuses are connected and are together termed the **lumbosacral plexus.** As in the case of the frog the various branches contain sensory nerve fibers to the skin and motor nerve fibers to the muscles.

5. THE SPINAL REFLEX

A **reflex** or **reflex act** is a simple act which conforms to a definite pattern when the stimulus required to evoke it is applied. A **spinal reflex** is one which occurs independently or in the absence of the brain. Spinal reflexes can be easily shown experimentally in the frog. The spinal cord is cut across behind the brain and the brain is destroyed or the dorsal portion of the head is cut off leaving the lower jaw in place. The frog is then suspended by a hook through the lower jaw. When the experiment is carefully performed and the frog is otherwise in good condition it will make no spontaneous movements, i.e., movements not in direct response to a stimulus. If, however, the skin of one side of the body is irritated by placing on it a small piece of paper saturated with dilute acid, the hind leg of the same side will be moved up and the paper will be pushed away. This is only one of many different spinal reflexes. Such spinal reflexes conform to a definite pattern of movement — a pattern which has its counterpart in the arrangement of the neurons in the reflex arc.

Corresponding to the pattern of behavior expressed in the reflex act there is in the nervous system a definite arrangement of neurons along which nerve impulses pass and give rise to the reaction. This is called the **reflex arc** (Fig. 32:2). In the example chosen the impulse starts in the terminal branches of the dendrites of sensory neurons ending in the skin of the frog. It passes in the dendrites which may form part of a spinal nerve toward the dorsal ganglion. In the dorsal ganglion the impulse need not, apparently, pass through the cell body but may go directly to the axon and through it in the dorsal root of the spinal nerve to the spinal cord. The terminal branches of the sensory neuron end in the dorsal column of the gray matter. To continue its course the impulse must pass through a synapse to the dendrites of a **correlation neuron** which carries it to the ventral column. Another synapse must occur between the terminal branches of the axon of the correlation neuron and the dendrites of a motor neuron. In the motor neuron the impulse is carried to the muscles of the leg and stimulates them to contract. It should be understood that in an actual reflex the reflex arc usually consists of several neurons of each type conducting in parallel. Thus the area of the skin stimulated may be such that a number of sensory neurons are stimulated which in consequence transmit nerve impulses to a number of correlation neurons which in turn transmit them to a number of motor neurons. Also there may be two or more correlation neurons arranged in series so that the impulse passes successively through them, although it never passes through more than one sensory neuron and one motor neuron. Some of the correlation neurons cross the spinal cord so that the impulse may be transmitted to a motor neuron on the opposite side.

6. THE BRAIN

The central nervous system (brain and spinal cord) arises on the dorsal side of the embryo from the outer germ layer or embryonic skin as a long groove which later, owing to the folding over of the edges of the groove, becomes a tube called the **neural tube.** In the case of the spinal cord the walls of the tube become much thickened and the cavity is reduced to the small central canal, but the general plan of a more or less uniform tube remains. In the brain, however, the thickening of the walls is not uniform and the cavity of the tube becomes enlarged in certain places. In the first indication of the brain in the embryo there are three such enlargements separated by constrictions. The enlargements are called the **fore, mid,** and **hind brains** (Fig. 36:6). Later in development, constrictions appear in the fore and hind brains so that the entire brain becomes divided into five divisions. The term **encephalon** is applied to the brain as a whole and the names of the five parts are made by using the following prefixes: *tel* = end, *di* = between, *mes* = middle, *met* = after, and *myel*, which indicates a relation to the spinal cord. Thus the different divisions of the brain named from anterior to posterior are:

I. Telencephalon
II. Diencephalon
III. Mesencephalon
IV. Metencephalon
V. Myelencephalon

It is not possible to assign precise functions to each of the five divisions of the brain, but it may be said, in general, that the higher the animal in the vertebrate scale, the greater is the development of the more anterior divisions, especially the telencephalon, and that the more posterior divisions, especially the metencephalon, are concerned with the simpler and more primitive activities of the animal.

A. THE FROG'S BRAIN

We may now turn to a description of the brain of the adult frog (Fig. 32:5). At the extreme anterior end the **telencephalon** is produced to form two **olfactory lobes** from which the olfactory nerves pass to the **sensory epithelium** of the olfactory sacs. They are concerned with the sense of smell. The greater part of the telencephalon consists of the **cerebral hemispheres,** two relatively large, elongated, rounded bodies. In the frog the cerebral hemispheres seem to be chiefly concerned with the conduction of nerve impulses from the olfactory lobes to the diencephalon (see next paragraph). Each cerebral hemisphere contains a cavity or **lateral ventricle** which is continuous with the cavity of the diencephalon, called the **third ventricle,** through an opening called the **foramen of Munro.**

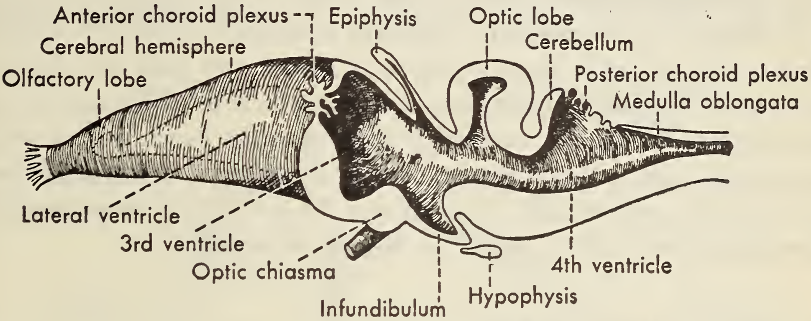

Fig. 32:5 Longitudinal, vertical section through the brain of a frog, drawn by B. B. Root from Hegner, *College Zoology*, The Macmillan Company.

The anterior portion of the roof of the **diencephalon** takes the form of a highly vascular membrane called the **anterior choroid plexus** which is folded into the cavity of the third ventricle and undoubtedly contributes to the nourishment of this part of the brain. From the posterior portion of the roof a minute fingerlike structure called the **epiphysis** projects toward the skull, possibly the vestige of a single median eye. The **optic nerves** from the eyes enter the brain on the ventral side of the diencephalon. As they enter the fibers cross to opposite sides of the brain forming the **optic chiasma.** The right and left sides of the diencephalon are somewhat thickened and form the **thalami** (singular **thalamus**), over which the fibers of the optic nerves spread out fanwise. Behind the optic chiasma the floor of the diencephalon extends ventrally, forming a funnel-shaped structure called the **infundibulum.** Connected with this posteriorly is the **hypophysis** or **pituitary body,** an important endocrine which is discussed in a later chapter. In addition to the special functions of the particular parts referred to, the main part of the diencephalon formed by the thalami seems to be concerned chiefly with correlation and transmission of nerve impulses received from the nasal capsules and the eyes (see later section on amphibian brain).

The roof of the **mesencephalon** is formed by two rounded projections called the **optic lobes.** The optic lobes are said to inhibit spinal reflexes. Its floor is formed by the **crura cerebri.** Its cavity is a narrow channel called the **iter.**

The **metencephalon** is a relatively short part of the brain in the frog. The **cerebellum,** which forms the roof, is a transverse thickening just behind the optic lobes.

The **myelencephalon** connects the brain with the spinal cord. Its roof is formed by the **posterior choroid plexus,** a vascular membrane similar to the anterior choroid plexus. Its floor and sides are thick and constitute the **medulla oblongata.** The medulla is a very important part of the brain in the frog. When all of the rest of the brain is removed the frog can still leap, swim, capture and swallow food, breathe normally, and live for a considerable time. When the medulla is removed death follows soon. Its cavity is called the **fourth ventricle.**

B. THE HUMAN BRAIN

In the frog the axis of the brain is continuous with that of the spinal cord, the two forming a rodlike structure enlarged and pointed at the anterior end. In man, on account of his erect posture, the axis of the brain makes three vertical bends or **flexures** (Fig. 32:6). The first of these, the **cervical flexure,** occurs where the spinal cord joins the myelencephalon and is toward the anterior or ventral side; the second, the **pontine flexure,** occurs in the metencephalon and is in the opposite direction toward the posterior or dorsal side; the third, the **cephalic flexure,** occurs in the midbrain and is directed toward the anterior or ventral side. The axis of the brain thus forms a letter Z on top of the spinal cord (Fig. 32:6).

The **telencephalon** of the human brain exceeds in size all the other parts. When the brain is viewed from above only the **cerebral hemispheres** are visible, all the other parts being hidden by their massive lobes. A deep depression, the **longitudinal fissure,** separates the two hemispheres. Each hemisphere is divided into five lobes. Numerous smaller fissures divide the surfaces of the lobes into **convolutions.** The **olfactory lobes** are small and hidden under the cerebral hemispheres. Each cerebral hemisphere contains a cavity or ventricle which, as in the frog, communicates through an opening, the **foramen of Monro,** with the third ventricle. The two hemispheres are held together above the third ventricle by a fibrous band called the **corpus callosum** (Fig. 28:3). The outer portion of the cerebral hemispheres or **cerebral cortex** consists of a layer of gray matter containing numerous nerve cell bodies and their processes (dendrites and axons). Within the cortex and developed chiefly on the lateral and basal (morphologically ventral) walls are other masses of nerve cell bodies and nerve processes, chief among which is the **corpus striatum.**

The **diencephalon** is completely covered by the cerebral hemispheres. As in the frog there is an **anterior choroid plexus, pineal body, optic chiasma, infundibulum,** and **pituitary body** (Fig. 32:6). As will be seen later the **thalamus** which occurs in the wall of the diencephalon is an important part of the human brain.

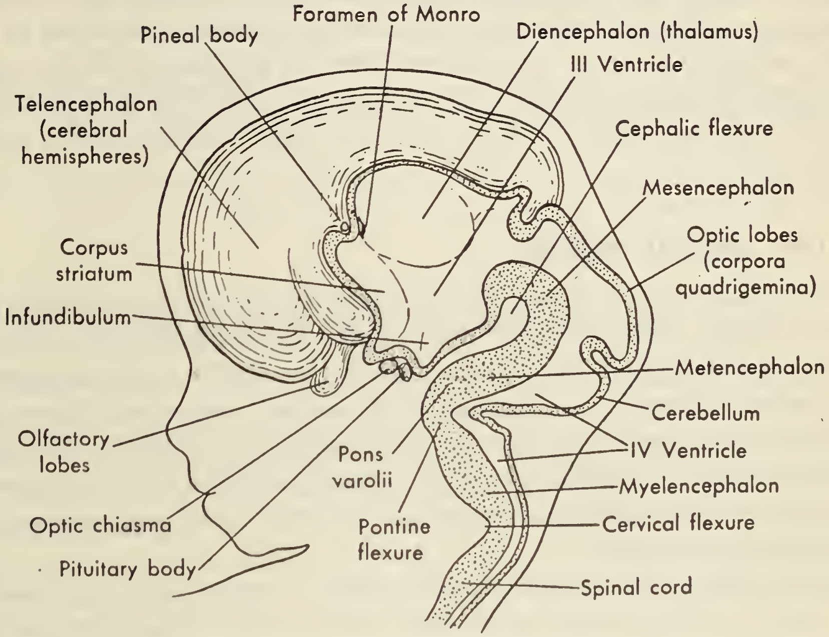

Fig. 32:6 A diagrammatic sagittal section of the head of a human foetus about the third month, showing the parts of the brain.

The **mesencephalon** is also relatively small. The roof is formed by four rounded bodies called the **corpora quadrigemina** which occupy the places occupied by the optic lobes in the frog. The corpora quadrigemina receive fibers from the optic and the auditory nerves. The floor is formed by the **crura cerebri.**

In the mesencephalon and diencephalon sensory impulses received in the cranial and spinal nerves are relayed to the cerebrum and cerebellum and motor impulses are distributed.

Next to the telencephalon the **metencephalon** is the most prominent part of the human brain. The **cerebellum** is relatively large. It consists of right and left hemispheres connected by a central portion called the **vermis.** The floor is formed by the **pons Varolii.** This is a region where many fibers cross from one side to the other of the brain.

The roof of the **myelencephalon** is formed by the **posterior choroid plexus** as in the frog. The **medulla oblongata** or bulb which forms the floor and sides is a pathway for nerve fibers passing to and from the spinal cord to the other parts of the brain. It has, however, other important functions. In man it contains the centers, i.e., the groups of nerve cells, which control the following simple reflexes — closing the eyelids, sneezing, coughing, mastication, swallowing, vomiting, secretion of the saliva and gastric juices. It also sends fibers to the ganglia of the parasympathetic system (see Sec. 9 of this chapter) controlling the respiratory movements, contraction of the walls of the blood vessels, and the action of the heart.

7. THE CRANIAL NERVES

The cranial nerves, although they arise from the brain in symmetrical pairs, are not connected with it at regular intervals as are the spinal nerves with the spinal cord. Some of them are entirely sensory and some are "mixed nerves," i.e., contain both sensory and motor fibers and some are motor nerves. In the case of the sensory nerves there are ganglia corresponding in a general way to the dorsal ganglia of the spinal nerves, but they are not regularly arranged and in some cases the ganglion cells are in the sense organs.

In the frog there are ten cranial nerves. In man there are twelve, the last two, the eleventh and twelfth, being really spinal nerves whose connections have been moved up into the brain. The connections and functions of the first ten cranial nerves are so similar in the frog and in man that for our present purpose one description will serve for both. The nerves are numbered from anterior to posterior and Roman numerals are usually used.

TABLE 32:1. THE CRANIAL NERVES

I. **Olfactory Nerve.** Purely sensory. Its fibers arise from sensory cells in the olfactory membrane of the nasal cavity.

II. **Optic Nerve.** Purely sensory. Its fibers arise from cells in the retina of the eye

III. IV. VI. Motor nerves to the muscles of the eyeball. Entirely motor. Their fibers arise from cells in the brain

V. **Trigeminal Nerve.** Sensory and motor. Its sensory fibers come from the face, including the anterior half of the scalp, the lips, teeth, mouth, and the anterior part of the tongue. Its motor fibers innervate the muscles of mastication

VII. **Facial Nerve.** Sensory and motor. Its sensory fibers come from the tongue. Its motor fibers innervate the muscles determining the facial expression

VIII. **Auditory Nerve.** Entirely sensory. Its fibers pass from the internal ear to the brain. Part of its fibers arise in the organ of hearing, another part arise in the organ of equilibrium

IX. **Glossopharyngeal Nerve.** Sensory and motor. Innervates the tongue and pharynx

X. **Vagus Nerve.** Sensory and motor. The name, which means "the wanderer," refers to its wide distribution to the pharynx, esophagus, stomach, respiratory organs, and heart

XI. **Spinal Accessory.** Motor. Innervates pharynx, esophagus, stomach, intestines, and respiratory organs. Occurs as a small branch of nerve X in the frog

XII. **Hypoglossal Nerve.** Motor. Innervates the muscles of the tongue. Found in man as a cranial nerve which corresponds to the first spinal nerve in the frog

8. THE MECHANISM OF THE SPINAL CORD AND BRAIN

The activities of the spinal cord and brain are carried out by their nerve cells or neurons. Hence it is to the differentiation of the cells and their interrelations that we must turn for an explanation of the working of these organs. Many painstaking and laborious investigations have contributed to give us a detailed picture of the course which the various types of nerve fibers take through the brain and spinal cord and the interrelations which they establish. It is possible here to consider only a few simple cases.

A. NERVE FIBER TRACTS IN THE AMPHIBIAN BRAIN

The brain of the mud puppy, *Necturus*, is similar to that of the frog. The diagram (Fig. 32:7) shows some of the paths which the nerve impulses may take when the sensory cells of the eye or ear are stimulated. These may be called **cranial reflex arcs** and the reactions involved may be called **cranial reflexes.**

When sensory cells of the ear are stimulated the impulses are carried in the fibers of the eighth nerve to the medulla oblongata. There the impulses pass to neurons of another type (A) and are relayed to the roof of the mesencephalon where they pass to neurons of still another type (B). These neurons send fibers anteriorly into the diencephalon (thalamus) and posteriorly through the brain to the spinal cord. Should the impulses take the posterior path they may pass to motor neurons of the third nerve and stimulate the muscle fibers of one of the eye muscles to contract, or they may pass to motor neurons of the fifth nerve and stimulate the fibers of one of the muscles of the jaw to contract, or to motor neurons of the seventh nerve and activate one or more of the facial muscles, or lastly they may pass down into the spinal cord and passing to motor neurons in the ventral horn of the gray matter cause one or more of the body muscles to contract. On the other hand, should the impulses take the forward path, they may pass to neurons (C) in the thalamus. The axons of these neurons pursue a path similar to that pursued by neurons B and the impulses may take any one of the motor paths already indicated.

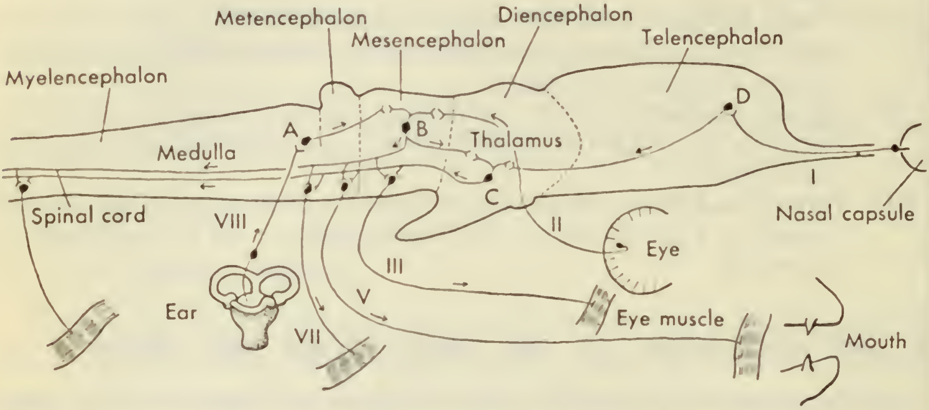

Fig. 32:7 Diagram of some conduction paths in the brain of *Necturus*, seen in longitudinal section. For a description of the pathways taken by the nervous impulses when the sensory nerves from the olfactory capsule, eye, or ear are stimulated, see the text. After C. J. Herrick, *Brains of Rats and Men*, University of Chicago Press.

Sensory nerve impulses from the eye come to the brain along the fibers of the optic nerve and over the optic tracts in the diencephalon to the roof of the mesencephalon (optic lobes). There the impulse may pass to neurons of the same type (B) which received the impulses from the ear. From here the same paths are open to these impulses as were open to the impulses from the ear.

Another type of neuron is found in the cerebral hemispheres. Axons from these neurons pass to the thalamus. They may send impulses to the neurons of type C already referred to and cause any one or a number of the motor activities to which reference has already been made. Nerve impulses may come to the cerebral hemisphere in the fibers of the olfactory nerve from the sensory cells of the nasal epithelium.

It should be noted that only certain of the possible paths in the *Nec-*

turus brain are indicated, there being many others. Just what determines which path a given nervous impulse will follow is not at present known. Undoubtedly the physiological state of the animal, especially its nervous state at the time of receiving the stimulus, and its previous nervous activity are factors.

B. CONDITIONED REFLEXES

In a now famous series of experiments on dogs Pavlov[1] investigated what he called the **conditioned salivary reflex.** When a dog tastes food the stimulus causes the salivary gland to secrete saliva. This is a natural, unconscious reflex. The activity of the salivary gland can be measured by connecting a fine glass tube or canula to the duct of the gland and observing the rate at which the saliva flows.

If a bell is rung every time the dog is fed after a time it will be found that there will be a flow of saliva when the bell is rung even if the dog is not given food. The dog is then said to be conditioned to the ringing of the bell and a new kind of reflex has been developed in which the ringing of the bell causes saliva to flow. It is possible to trace the path followed by the nerve impulse in both the "natural reflex" and the conditioned reflex.

In the case of the natural reflex the path is as follows (Fig. 32:8): The food stimulates the taste buds in the tongue and the nerve impulses are carried in the sensory fibers of the seventh nerve to the primary gustatory center in the medulla. The impulses now pass to neurons (B) which relay the impulses to neurons in the salivatory center. The axons of these neurons form part of the seventh nerve and go to the submaxillary ganglion where the impulses are passed to other neurons which stimulate the salivary gland to secrete. This reflex arc is present in the animal at birth and the animal does not have to learn to secrete saliva when it tastes food.

There is also a natural reflex in response to ringing the bell which is as follows: From the cochlea (the auditory portion of the ear, see Chap. 33) the nerve impulse passes along the eighth nerve to the primary auditory center also in the medulla. Here the impulses pass to neurons (A) which go down the spinal cord to motor neurons in the ventral horn of the gray matter. In these neurons the impulses may pass to one of the neck muscles causing the head to be moved in the direction of the sound. This is also not a learned reflex.

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[1] Pavlov, I. P., *Conditioned Reflexes*, translated by G. V. Anrep, Oxford University Press, Oxford, 1927.

There is no direct connection between these two reflex paths and s the secretion of saliva does not naturally follow auditory stimulation. These simple paths are not, however, the only paths which the impulses may take. In the case of the salivatory reflex, neurons whose cell bodies are in the primary gustatory center may carry the impulses to a correlation center where they may pass to other neurons (C) and be relayed to still other neurons which carry them to the salivatory nucleus. This path may also occur in the "natural" salivatory reflex. A similar path through the correlation center leads from the primary auditory center through the neuron (D) to the ventral horn of the spinal cord. This also may be involved in the "natural" reflex. However the neurons, D, send processes

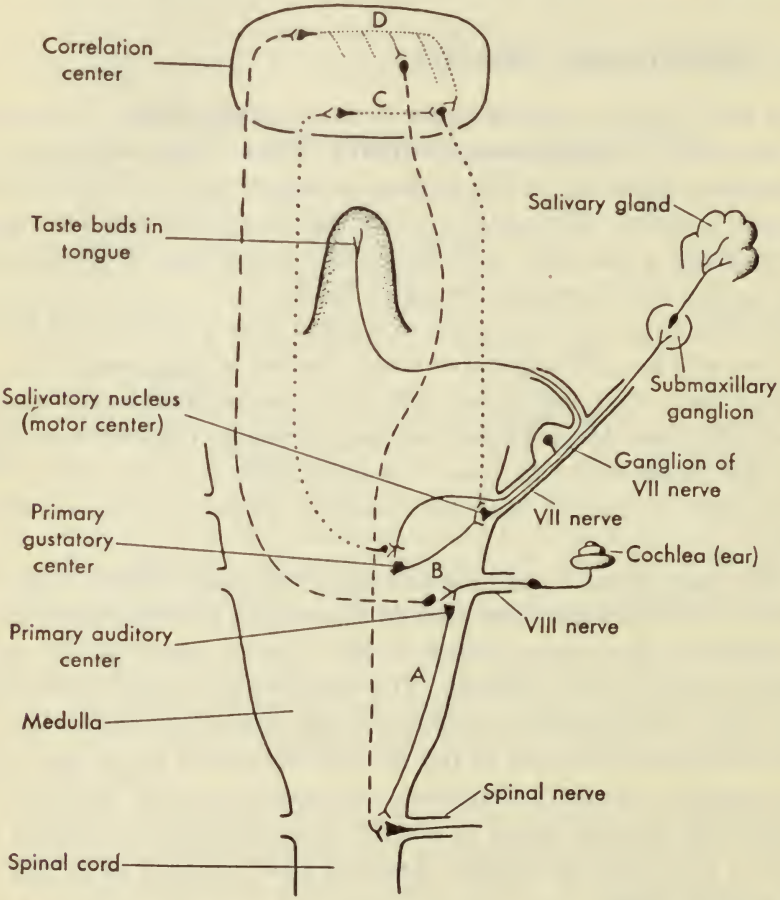

Fig. 32:8 Simplified diagram of a conditioned reflex. The primary (unconditioned) taste-salivatory and auditory-head-turning arcs are shown in continuous lines. The secondary loop of the auditory arc going to the correlation center is shown in interrupted lines. The similar loop of the gustatory arc is shown in dotted lines. After C. Judson Herrick, *Brains of Rats and Men*, University of Chicago Press.

to various parts of the correlation center and some of these can synapse with neurons sending axons to the salivatory nucleus. This does not usually occur, but as the experiments show by repetition of the two stimuli simultaneously, a path may be established which connects the primary auditory center with the salivatory nucleus; this is what happens when the animal has been conditioned to respond to the bell by secreting saliva.

C. THE EVOLUTION OF THE TELENCEPHALON

The cerebral hemispheres of fishes and amphibians are chiefly concerned with receiving and correlating stimuli received in the olfactory nerves. Cerebral cortex and corpus striatum are absent from the telencephalon.

In reptiles and birds the corpus striatum is well developed. It is a correlation center for reflexes, particularly those involving the eye and ear. The cerebral cortex is present but is more simply organized and more intimately connected with the corpus striatum than in the mammalian brain. In the reptiles evolution evidently took two divergent directions: one leading to the birds, the other to the mammals. In birds the enlargement and complication of the corpus striatum reaches its climax in the vertebrate series. As is well known, sight and hearing are exceptionally well developed in birds, and reflexes involving the eye and ear play a large part in their behavior. On the other hand the cerebral cortex shows a relatively simple organization.

In mammals the corpus striatum is well developed but its development is overshadowed by that of the cerebral cortex which takes on distinctive characters. The nonolfactory portion of the cortex which is present in reptiles is much larger in mammals, and the cells show many local differences in the form and arrangement of their cell bodies.

In man the cerebral cortex shows a quite exceptional development. It makes up about half the total weight of the brain. From a purely anatomical point of view it is one of the most distinctive and characteristic structures of the human body. Physiologically it is even more remarkable. It controls the activities not only of the remainder of the nervous system but through it the entire organism. The cells (Fig. 4:14) are arranged in layers, as many as ten of which can be distinguished in some regions. Numerous (fifty or more) cortical areas have been distinguished, differing in the structure and arrangement of the nerve cells.

Every neuron of the cerebral cortex is enmeshed in a tangle of very fine nerve fibers of great complexity, some of which come from very remote parts. It is probably safe to say that the majority of the cortical neurons are directly or indirectly connected with every cortical field. This is the anatomical basis of cortical associational processes. . . . And in the cortical association centers it is the capacity for making this sort of combination and recombination of the nervous elements that determines the practical value of the system.

When the visual area of the cerebral cortex is activated following the stimulation of the retina by some particular field of view, it is safe to say that at least a million cortical nerve cells are directly stimulated by the nervous impulses which discharge into this cortex from the optic thalamus. These million cells activate other millions, and so on in indefinite series, and the aggregate of the connections actually made in any extended associational process is evidently an enormous number.[1]

9. THE AUTONOMIC NERVOUS SYSTEM

Connected with the brain and spinal cord is a system of nerves and ganglia, called the **autonomic system,** which is chiefly concerned with the control of the movements and other activities of the viscera. Unlike the brain and spinal cord this system seems to involve only motor nerves. In the thorax and abdomen a double chain of ganglia runs near and parallel to the vertebral column. The ganglia are connected with the spinal cord by the visceral rami already referred to when describing the spinal nerves, and send nerves to the various viscera, heart, lungs, stomach, intestine, kidney, bladder, and so forth. The fibers from the ganglia go directly to the various organs and terminate in them. In some cases, e.g., the heart, the organs are stimulated to increased activity; in other cases, e.g., the stomach, the effect is to slow down or stop muscular contraction. These ganglia and nerves form the **sympathetic system.** Nerve cells in the midbrain and medulla send out axons which travel in the third, seventh, ninth, and tenth cranial nerves and go to internal organs. The terminal branches of these axons synapse with neurons in the organs. In some cases, e.g., the heart, the activity of the organ is inhibited, in other cases, e.g., the salivary gland, it is accelerated. A similar system of neurons connects the sacral region of the spinal cord with the pelvic viscera. These two systems are together called the **parasympathetic system.** A third group of ganglion cells and nerves is located in the walls of the viscera. These constitute the **enteric system.** A peculiarity of the autonomic nervous system is that it contains not only nerves which stimulate to activity but also nerves which inhibit the activity of the organs. The autonomic system affects and is affected by the emotions, and also as we shall see in a later chapter by certain endocrine secretions.

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[1] C. Judson Herrick, *Brains of Rats and Men*, the University of Chicago Press, Chicago, 1926.

Topical Outline of Chapter 32

1. The nerve cell or neuron 618
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    A. The frog's brain 628
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    B. Conditioned reflexes 635
    C. The evolution of the telencephalon 637
9. The autonomic nervous system 638

Questions

1. Describe a motor neuron. State in what respects it differs from a typical cell. How are these differences related to its special functions?
2. State some of the changes which occur in a nerve when an impulse passes along it.
3. Describe a cross section of the spinal cord of man. Where are most of the nerve cells located?
4. Trace the path of a spinal reflex.
5. Name in order the five divisions of the brain and briefly describe each part.
6. Describe the distribution of the twelve cranial nerves in man.
7. Explain how a conditioned reflex may be established.
8. Briefly discuss the relations and functions of the autonomic nervous system.

Suggestions for Further Reading

Lickley, James Dunlop, *The Nervous System*, an elementary handbook of the anatomy and physiology of the nervous system for the use of students of psychology and neurology, Longmans, Green & Company, New York, 1916.

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CHAPTER 33

The Sense Organs

A sense organ is sensitive to a particular kind of stimulus, such as light, and relatively insensitive to other kinds of stimuli. This stimulus it transforms into a nervous impulse which is transmitted in a sensory nerve to a group of nerve cells in the brain or spinal cord. Thus the sense organ selects the stimulus from among all the many different kinds of physical changes which occur in its environment. However, the kind of sensation which the person experiences, i.e., whether that of sight, hearing, smell or some other, depends on the part of the central nervous system to which the nerve impulse is transmitted. Thus when the optic nerve is stimulated the person receives the sensation of sight, and when the auditory nerve is stimulated he receives the sensation of hearing. No kind of stimulation of the auditory nerve will produce the sensation of sight nor will any kind of stimulation of the optic nerve produce the sensation of hearing.

1. NOSE, MOUTH, AND THE BODY IN GENERAL

The **nasal cavities** of both the frog and man are partly lined with a moist, sensitive olfactory membrane composed of epithelial cells. Among these epithelial cells are the **sensory cells** (Fig. 33:1), elongated, ciliated cells, continued internally into fine nerve fibers, which together with those from the other sensory cells make up the olfactory nerve.

The cavity of the **mouth** is also lined with a moist membrane which contains sensory cells. Here, however, they tend to be collected in groups forming taste buds, which are especially numerous on the tongue. Although resembling the sensory cells of the olfactory epithelium the sensory cells of the taste buds do not give rise to nerve fibers. Fine processes from sensory branches of cranial nerves VII and IX surround them and transmit the nerve impulses to the brain.

Throughout the body in the skin, muscles, walls of the digestive tube, and in fact everywhere, sensory cells occur which receive and transmit special stimuli, such as heat, cold, pressure, and fatigue. These stimuli are each received and transmitted by special sensory cells so that a cell which is sensitive to heat, i.e., a rising temperature, is under ordinary circumstances insensitive to cold, i.e., a decrease in temperature. These sensory cells take on various special forms according to the stimuli to which they respond, and are surrounded or otherwise associated with fine fibers from sensory branches of spinal or cranial nerves.

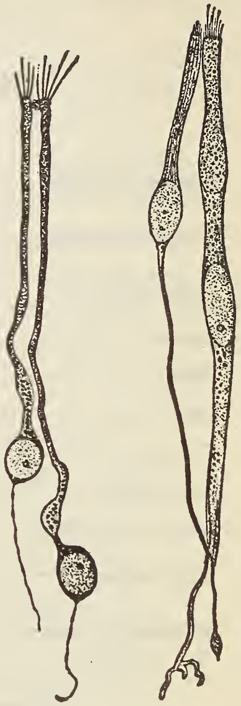

Fig. 33:1 Olfactory cells from the lining of the nasal cavity of the frog. On the left, two sensory cells with ciliated outer ends, enlarged nuclei, and fine basal fibers; on the right, two interstitial cells. From Holmes, *Biology of the Frog*, The Macmillan Company.

2. THE EYE

The large eyes of the **frog** protrude from either side of the head and look sidewise so that their vision covers entirely different fields. Each eye lies in an **orbit** or eye socket into which it can be withdrawn and covered by the eyelids. The **upper eyelid** is capable of only a slight downward movement, but the **lower eyelid** can be drawn up to cover the remainder of the exposed part of the eye. The lower eyelid is in reality composed of two parts, a **lower eyelid proper,** which forms the thicker lower portion and a **nictitating membrane,** a thinner and more transparent upper portion, separated from the lower eyelid proper by a shallow groove. In the center of the eye is a dark oval, the **pupil.** This is really the transparent window through which light passes to the interior sensitive part of the eye. Surrounding the pupil is an iridescent ring, the **iris,** and surrounding the iris, **the white of the eye** extends outward to the eyelids.

The **human eyes** lie in the orbits protected above by the eyebrows. The upper and lower eyelids close the eyes, most of the movement being in the upper eyelid. From the margins of the eyelids rows of hairs, the **eyelashes,** project. The eyelids are covered externally by the skin and internally by a moist sensitive membrane, the **conjunctiva,** which is reflected from the inner surface over the front of the eyeball. The conjunctiva is kept moist and transparent by the secretion from the tear gland or **lacrimal gland** which is poured out through a number of minute ducts on the inner or conjunctival surface of the upper lid, and distributed by the winking of the eyelid. Ordinarily the secretion of the lacrimal gland in excess of that required to keep the eye moist is carried away by the **lacrimal canal** which opens into the nose. When the conjunctiva is irritated or the person experiences intense emotion the secretion may be in excess of that which can be carried away by the canal and tears flow over the cheeks.

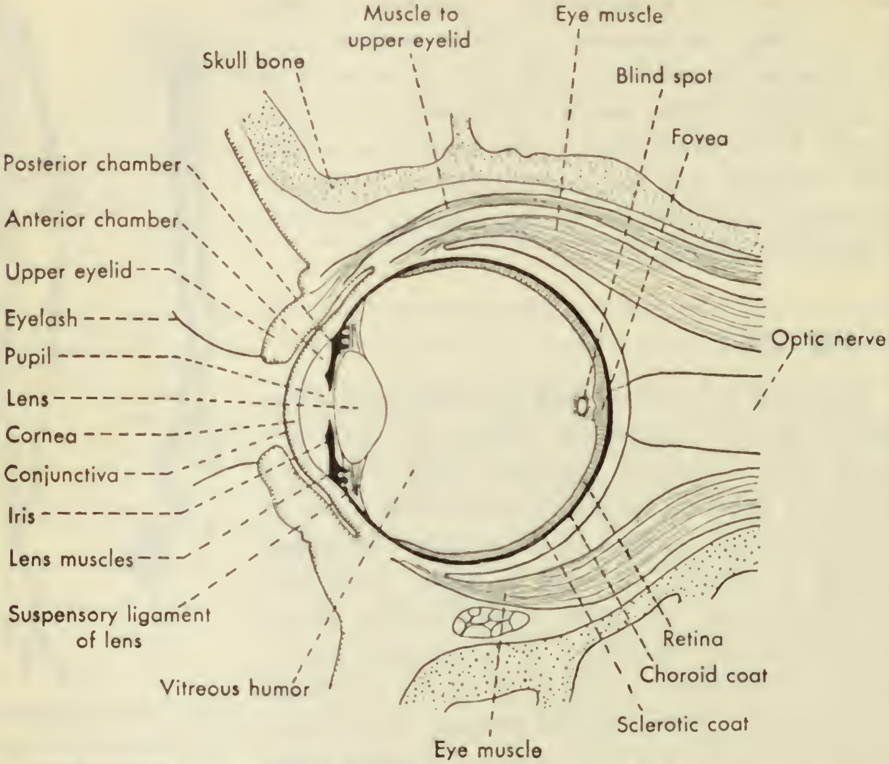

Fig. 33:2 The structure of the human eye. The eye has been sectioned vertically through the center of the pupil and the center of the fovea, i.e., through the optic axis. The observer is looking into the right side of the left eye. The optic nerve enters the eye on its median, i.e., nasal side, and gives rise to the blind spot seen in the diagram on the inside of the retina. When the eye is directed at an object the optic axis is placed in line with it and the object is centered on the fovea. Slightly modified after L. L. Woodruff, *Animal Biology*, The Macmillan Company.

The internal structure of the frog's eye is essentially similar in its main features to the human eye. The following description applies to the eye of man. The eyeball is moved in the orbit and the direction of vision controlled by six **eye muscles.** The **superior** and **inferior recti muscles** direct it up and down respectively; the **internal** and **external recti**

muscles move it toward and away from the nose, and the **superior** and **inferior oblique muscles** roll it on its axis. It should be remembered that in normal vision the movements of the two eyeballs are **coordinated** so that when the internal rectus of the left eye contracts, the external rectus of the right eye contracts to a corresponding extent.

The internal structure of the eye may be studied in a longitudinal section passing through the lens and the fovea (Fig. 33:2). Such a section shows the three coats of the eyeball. The outer of these, the **sclerotic,** is a firm, opaque, white coat, composed of connective tissue; it is continued over the anterior portion of the eyeball as the transparent **cornea.** Next comes the **choroid coat.** This coat contains most of the blood vessels of the eye. Anteriorly it becomes separated from the sclerotic and forms the **iris** in the center of which is the opening called the **pupil.** The iris is pigmented and is the part of the eye referred to when a person is said to have blue or brown eyes. The iris acts as a diaphragm and determines how much light enters the eye through the pupil. In dim light the pupil is large, in bright light it is small. Within the choroid coat and forming the lining of the posterior half of the eyeball is the **retina.** This is the thinnest of the three coats and contains the nerve cells. Just behind the iris and attached to the choroid by a **suspensory ligament** is the **lens.** A line drawn through the center of the pupil and the lens and to the center of the retina is called the **optic axis.** Where the optic axis intersects the retina is a small area called the **macula lutea** in the center

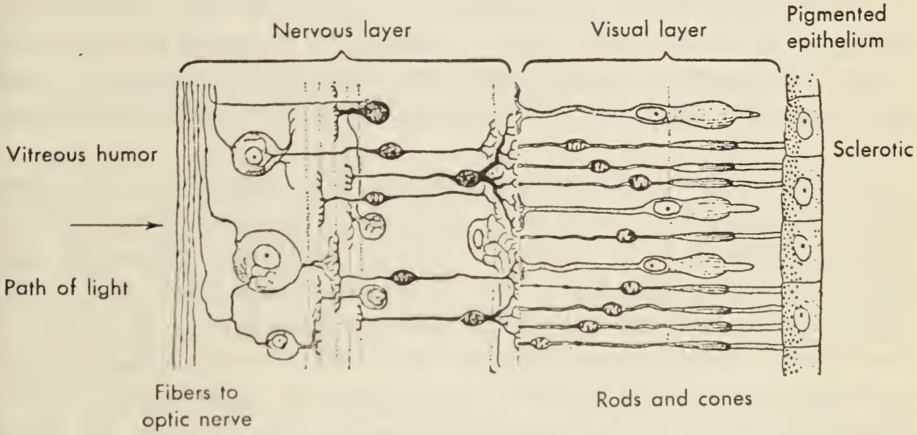

Fig. 33:3 Section of the human retina. In the eye, the left side of the section is toward the lens so that the light passes through the fibers of the optic nerve and the nervous layer before reaching the rods and cones. The neurons of the first layer are in the part labeled "visual layer"; those of the second and third layers and the association neurons are shown in the part labeled "nervous layer." The vitreous body is to the left, the choroid coat to the right. From L. L. Woodruff, *Animal Biology*, The Macmillan Company.

of which is a small depression called the **fovea centralis** where vision is most acute. When an object is looked at its image is formed on the macula lutea. A short distance from the fovea toward the nasal side is the "**blind spot**" where the optic nerve passes through the retina. The cavity in front of the lens is filled with a liquid called the **aqueous humor,** and the cavity behind by a jellylike substance called the **vitreous body.**

The eye may be compared to a photographic camera and the retina to a photographic film or plate on which is recorded a picture or image of the field of vision. As in a photographic camera the image on the retina is inverted. This, however, does not bother us because we are not conscious of what happens in the eye but only of the resulting sensation in the brain which we interpret in accordance with our other sensations, especially those of touch. The image is focused on the retina by the lens. In a camera focusing is accomplished by moving the lens back and forward. In the eye the same result is obtained by changing the curvature of the lens. In order to understand how this is brought about we must study somewhat more closely the lens and its relation to the choroid coat of the eyeball.

The lens of the human eye is a biconvex body about the size of a pea, but flattened so that the diameter along the optic axis is about half the vertical diameter. It is composed of living nucleated cells which take the form of transparent fibers. The whole structure is elastic and is held in place by the suspensory ligament which extends from its periphery to the choroid. This ligament holds the lens under a certain tension so that it normally tends to be flattened and adjusted for distant vision. In the choroid layer where the suspensory ligaments are attached are small **ciliary muscles.** The contraction of these muscles tends to relieve the tension exerted by the suspensory ligament on the lens which, therefore, becomes more convex and so adjusted as to form an image of a near object. The adjustment of the lens to form a sharp image on the retina is called **accommodation.** In **farsightedness** the lens does not become sufficiently convex. This is corrected by the use of convex "glasses" which make up for the lack of convexity of the lens. **Nearsightedness** is due to the lens of the eye being too convex. This is corrected by using concave glasses. Defective sight is often due to irregularities in the cornea or lens. **Astigmatism** is usually due to unequal curvature of the cornea, so that its surface is not spherical but resembles the back of a spoon.

The rays of light after passing through the cornea, the aqueous humor, the lens, and the vitreous body are focused on the retina. The retina consists of a number of layers of nerve cells and their nerve processes (Fig. 33:3). The sensory cells, called **rod** and **cone cells,** which receive the light stimulus are turned away from the light and toward the choroid coat. This is due to the fact that the retina is developed in the embryo as an outgrowth of the lateral wall of the brain (see the diagram of the development of the eye, Fig. 36:7). The rays of light, therefore, must pass through the other layers of the retina before reaching them. This does not interfere with vision because the nerve cells and fibers which overlie the sensory cells are almost completely transparent. Nearly everybody has become aware at some time of the minute blood vessels which run over the surface of the retina. On looking at a clear bright area they often appear as hazy transparent filaments resembling the hyphae of a fungus.

The rod and cone cells owe their names to the peculiar shapes of their ends. In the case of the rod cells the ends turned away from the light take the form of long, straight rods. In the cone cells the corresponding ends are shorter pointed cones. Cone cells are the only retinal structures present in the fovea, there being no rods there. Beyond the fovea in the macula are rod cells but they are fewer in number in this region than the cone cells. Beyond the macula the proportion of cone cells to rod cells diminishes toward the periphery of the retina where there are very few cone cells. The rods and cones differ in function. The cones are sensitive to fairly bright light and distinguish between the different colors of the spectrum, while the rods are sensitive to dim light and do not distinguish colors.

We will now consider the neurons or nerve cells through which the nerve impulses pass in going from the sensory cells to the brain. There are three layers of neurons in the retina. The rods and cones are thickenings of the dendrites of the outer or sensory layer. The axons of these **sensory neurons** extend toward the lens and divide into numerous fine branches in the proximity of the dendrites of the **neurons of the second layer.** The axons of these latter extend also toward the lens where they in turn branch and interlace with the dendrites of the **third layer of neurons,** called **ganglion cells.** The axons of the ganglion cells pass over the inner surface of the retina to collect at the blind spot where they form the **optic nerve** and go directly to the brain. Among the neurons of the second layer are neurons with processes running parallel to the surface of the retina. Any one of these neurons may receive nerve impulses from several rods and cones and transmit the combined effect to the neurons of the second or third layers.

3. THE EAR

A. THE FROG'S EAR

The eardrum or tympanum has already been referred to in considering the external features. It consists of a tightly stretched membrane on the side of the head posterior to the eye. Inside the eardrum is the cavity of the **middle ear** (Fig. 33:4). This is an air-filled cavity which communicates with the mouth through the Eustachian tube, the internal opening of which was referred to in describing the mouth cavity. The **internal ear** lies between the middle ear and the cranium and is lodged in the auditory capsule. It consists of a thin-walled sac, the **membranous labyrinth,** containing a fluid, the **endolymph,** and surrounded by another fluid, the **perilymph.** A small oval opening in the lateral wall of the auditory capsule between the inner and middle ear is closed by a small bone called the **stapes.** Extending from the stapes to the tympanum across the air-filled middle ear is a rod-shaped bone called the **columella.** Sound waves set the tympanum in vibration. The vibrations are transmitted by the columella to the stapes which passes them on in a magnified form to the perilymph of the inner ear. From the perilymph they pass to the endolymph of the membranous labyrinth.

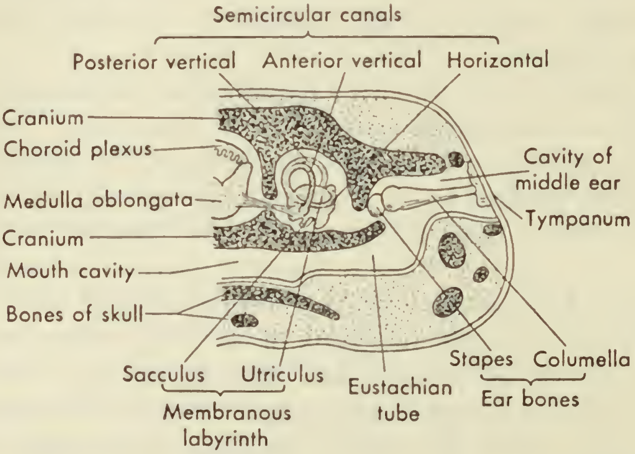

Fig. 33:4 A transverse section of the left side of the head of a frog showing the structure of the ear.

The **membranous labyrinth** is divided by a constriction into two portions, a lower saclike portion, the **sacculus,** and an upper irregular portion, the **utriculus.** The sacculus is the portion chiefly concerned with hearing. The membrane of both portions contains sensory cells. These are columnar epithelial cells with stiff, hairlike protoplasmic projections extending into the endolymph. The lower ends of these cells are surrounded by fine processes from the nerve fibers of the auditory nerve (VIII). It is believed that vibrations in the endolymph impinging on the protoplasmic processes stimulate the sensory cells and cause them to send out nerve impulses which pass to the fibers of the auditory nerve and thence to the brain. The frog is probably unable to recognize the different tones or qualities of sounds, his hearing being like that of a completely tone-deaf person.

The perception of sound is only one of the functions of the ear. The other, which is probably of more importance in the life of the frog, is concerned with perceiving and maintaining bodily equilibrium. Connected with the utriculus are three **semicircular canals** (Fig. 33:4) which run at right angles to each other; the **anterior** lies in a nearly vertical and obliquely anterior plane, a second, the **posterior,** extends in a vertical and obliquely posterior plane, a third, the **horizontal,** lies in a horizontal plane. At one end each canal is enlarged to form an ampulla which is well supplied with sense cells similar to those in the sacculus and similarly connected with the auditory nerve. Experiment has shown that after injury to one of the horizontal canals the frog tends to move in a circle and that after injury to one of the vertical canals it is unable to control its movements in a vertical direction. The semicircular canals are well shown in the ear of the pigeon (Fig. 33:5).

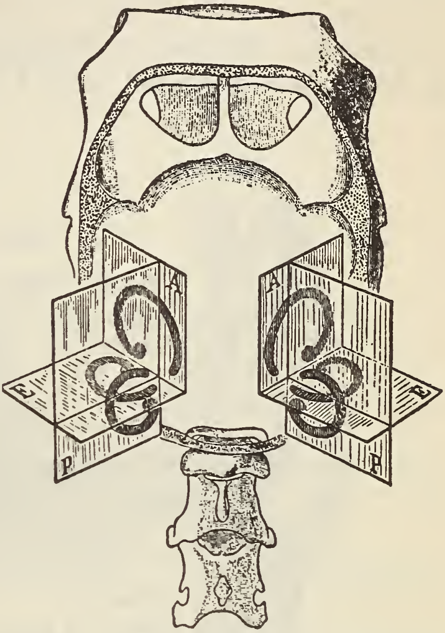

Fig. 33:5 The semicircular canals of the ear of the pigeon. A, plane of anterior or superior semicircular canal; P, plane of posterior canal; and E, plane of horizontal canal. After Starling, from Bainbridge and Menzies, *Principles of Human Physiology*, by permission of J. & A. Churchill.

B. THE HUMAN EAR

The human ear like that of the frog has two functions, the detection and analysis of sounds and the determination of the relation of the axis of the body to the direction of its movement and the direction of the pull of gravity on it. And, as in the frog, these two functions are carried out in different parts of the ear. In man the part of the ear devoted to the detection and analysis of sounds has become highly evolved.

The tympanum or eardrum lies at the end of a slightly curved canal about 1 inch in length and with an average diameter about equal to that of a lead pencil (Fig. 33:6). The external opening of this canal is surrounded by a structure usually called the **pinna** which probably helps to gather the sound into the canal. Two bones, the **malleus** (hammer) and **incus** (anvil), take the place of the columella in the frog and transmit the vibrations of the tympanum to the **stapes** (stirrup) and the inner ear. The three bones are articulated so that the actual vibrations of the tympanum are magnified in the stapes. The inner ear in man (and in most mammals and birds) is an exceedingly delicate instrument for the detection and analysis of sound. From the sacculus extends a long diverticulum, the **cochlea,** coiled in a shape resembling the shell of a snail. It is here that sounds are analyzed and the differences between high and low tones and the differences in the quality of sounds, e.g., the difference between a chord and a pure note, and between the same note played by a flute and a violin, are recognized. Exactly how these differences are determined in

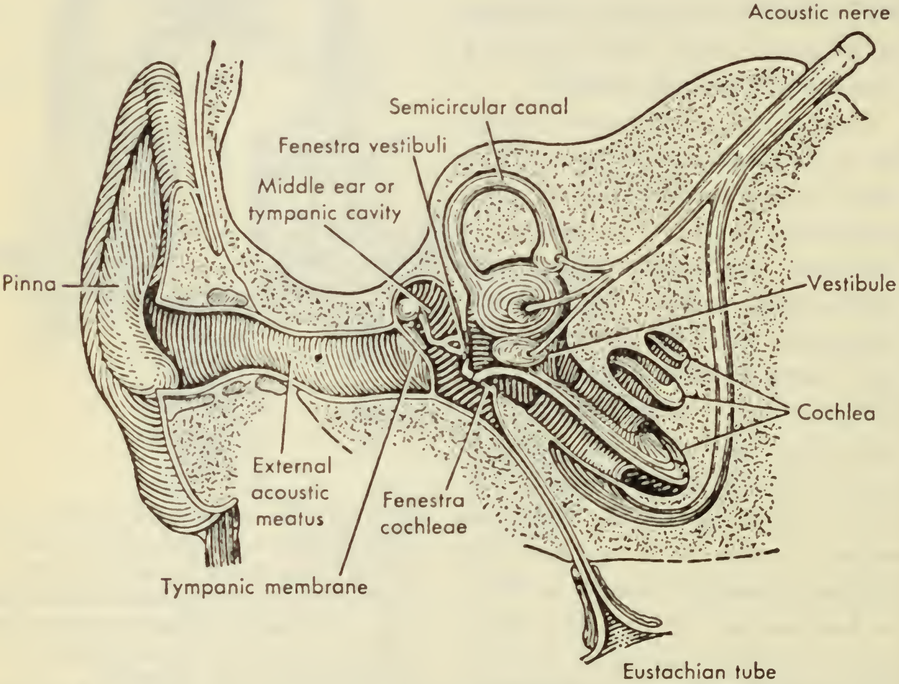

Fig. 33:6 Semi-diagrammatic section through the right ear. After Kimber, Gray, and Stackpole, from Hegner, *College Zoology*, The Macmillan Company.

the ear is not known. The utriculus and semicircular canals are similar in man and the frog, as indeed they are in nearly all vertebrates.

Topical Outline of Chapter 33

1. Nose, mouth, and the body in general 640
2. The eye 641
3. The ear 646
    A. The frog's ear 646
    B. The human ear 647

Questions

1. What is the difference between the sense cells in the nose and mouth?
2. Compare the external features of the eye of the frog with those of man. How are they related to the mode of life of the two animals?
3. Compare the human eye with a photographic camera. Carry the comparison as much into detail as you can.
4. Trace the path of a ray of light passing from an external source to the retina.
5. Trace the path of a nervous impulse from a rod or cone in the retina to the brain.
6. Explain how certain defects in sight can be corrected by lenses.
7. Explain how the ear carries out two independent and different sensory functions.
8. Compare the general features of the frog's ear with that of man and relate the differences to their modes of life.
9. Describe how the sound is transmitted from the eardrum to the internal ear in man.

CHAPTER 34

The Endocrines

Reference has already been made to the substance **secretin** which is formed in the duodenum, carried in the blood stream, and absorbed by the pancreas, which is thereby stimulated to secrete the pancreatic juice. Secretin is one of a number of substances to which the general name **hormone** is applied and which are of great importance in the regulation of many of the vital processes of vertebrates. A **hormone** is a substance produced in some part of the body and carried in the blood or lymph to other parts of the body where its presence causes structural or functional changes. Hormones are also called **internal secretions** and the glands which produce them **glands of internal secretion** or **endocrine glands.** Since the hormone does not leave the gland by means of a duct the term **ductless glands** has also been applied to them. This latter term is, however, inappropriate since some glands, for example the pancreas, produce both an external secretion which leaves the gland by a duct, and an internal secretion which passes into the blood or lymph.

The knowledge of hormones is chiefly the result of experiments on animals and clinical observations coupled with pathological findings. In experiments on animals the gland is removed and the effect of the removal observed. An extract is then made from the glandular tissue and administered to the experimental animals. If the effects observed after the removal of the gland decrease or disappear after administering the extract the latter is assumed to contain the hormone. The extract may now be fractionated, i.e., divided into different parts by chemical methods, and the parts separately tested on animals in the same way that the first extract was tested. In this way after many laborious processes the hormone may be obtained in relatively pure form and crystallized out of the solution. Further chemical work may lead to the determination of the chemical composition and the graphical formula of the hormone. The way is then prepared for the development of methods of producing the hormone synthetically.

Hormones may be compared and contrasted with vitamins. Features in which hormones resemble vitamins are:

1. They both affect the metabolism of the body.
2. Both are effective in small amounts.
3. Both are carried in the blood.
4. Some hormones resemble some vitamins chemically.
5. Some hormones have been made synthetically.

Hormones differ from vitamins as follows:

1. Hormones are manufactured in the body by the endocrine glands.
2. Most, but not all, hormones cannot be absorbed through the digestive tract and must be injected into the body.
3. Too much of a hormone usually produces serious effects and may prove fatal.

Hormones are usually named and classified according to the glands or glandular tissue by which they are produced. A general table of the endocrines and their secretions is given on pages 654 and 655. The location of the glands in the body is indicated in Fig. 34:1. Because they have to be injected, most hormones must be obtained in the form of an extract relatively free from foreign proteins or made synthetically.

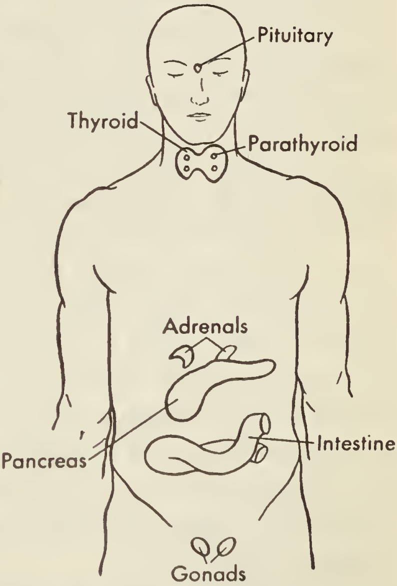

Fig. 34:1 The location of the ductless glands in the human body.

1. THE PANCREAS

Distributed through the pancreas among the cells which secrete the pancreatic juice are groups of peculiar cells forming small masses called the **islands of Langerhans.** These cells have been proved to produce an internal secretion called **insulin.** Insulin circulating in the blood controls the carbohydrate metabolism of the cells of the body. Underfunctioning or nonfunctioning of the islands of Langerhans causes a certain form of the disease called **diabetes** which is characterized by the excretion of sugar and the loss of glycogen from the liver. The condition can be corrected by the injection of insulin into the blood, but the injections have to be continued as long as the diabetic condition lasts. Overfunctioning of the islands of Langerhans or an excess of insulin in the blood gives rise to hunger and weakness. Insulin as usually prepared is a white powder, which can be obtained in a crystalline form. It is an organic compound, containing sulphur and probably allied to the peptides.

2. ADRENAL GLANDS

On the ventral side of each of the frog's kidneys is an irregular yellow streak, the **adrenal gland.** In man these glands are perched like cocked hats, one over the upper portion of each kidney, and on account of this position are called also **suprarenal glands.** The two human adrenal glands together weigh about ¼ ounce. The adrenal gland is composed of two different kinds of tissue, an outer yellowish portion, the **cortex,** and an inner brownish red tissue, the **medulla.** The medullary hormone or secretion of the medullary portion of the gland is called **adrenaline,** adrenine, or epinephrine. This hormone has been isolated from the medulla and obtained in a pure crystalline form. It is a relatively simple organic substance with the formula $C_9H_{13}NO_3$. Considered as a drug, adrenaline is astonishingly potent, a fraction of a milligram having an appreciable effect when injected into the human subject.

The general effect of adrenaline when passed into the blood from the adrenal glands is to prepare the body for the increased and more vigorous action which it may be called upon to exercise in an emergency. The heart beats more rapidly and more forcefully. The blood vessels of the muscles dilate while those of the skin and digestive tract constrict. In this way more blood is forced through the muscles. The lungs expand and contract more vigorously, increasing the supply of oxygen and releasing carbon dioxide more rapidly from the body. The liver discharges an increased amount of sugar into the blood stream. Thus the muscles are prepared to act to their greatest capacity. The adrenal medulla is stimulated to pass adrenaline into the blood under the emotional stresses of anger and fear.

The hormone of the adrenal cortex, called **cortin,** has been obtained as an extract but not as a chemically pure substance. Hence its chemical nature is not definitely known. The function or functions of cortin are not clearly understood. It is certain that its absence from the circulatory system causes Addison's disease, a wasting malady, which can be treated effectively only by the administration of the extract. There is some evidence that the cortical hormone affects the development and functioning of the reproductive organs in both the male and female.

3. THE THYROID GLAND

The thyroid gland is a soft, yellowish-red gland situated at the base of the neck (Fig. 34:1). Its shape and position have been compared to "a pair of well-filled panniers thrown across the back of a pack animal," the pack animal in this case being the trachea just below the larynx, the panniers the right and left lobes of the gland, and the sling the isthmus. It is richly supplied with blood vessels. The hormone secreted by the thyroid gland is called **thyroxine**. Its chemical formula is $C_{15}H_{11}O_4NI_4$. It can now be produced artificially and the synthetic product appears to be as efficient as that manufactured in the body. Thyroxine is peculiar among bodily products in containing a large amount of iodine, 65 per cent by weight.

If the thyroid gland is removed from young tadpoles they remain in the larval state and fail to metamorphose into frogs. If thyroxine is injected into the tadpoles metamorphosis occurs. If normal tadpoles are fed thyroxine metamorphosis occurs prematurely into small frogs. The chief function of the thyroid gland in mammals is believed to be to regulate the basal metabolism of the body. Since metabolism is necessary for the growth and differentiation of the cells, malfunction of the thyroid has marked and profound effects on the whole organism. Three different conditions may arise.

First, the thyroid gland may not be supplied with the materials required to manufacture its secretion. This occurs in various regions in the world where iodine seems to be lacking from the drinking water. One of the best known of these regions is the Swiss Alps and neighboring portions of Austria, Italy, Germany, and France. In the United States there is a so-called goiter belt around the Great Lakes and the upper Mississippi Valley. In response to this lack, the gland grows larger. The enlargement of the gland gives rise to a swelling in the neck called **goiter.** The condition is corrected by adding small quantities of iodine to the drinking water or table salt. The second condition arises from a deficiency or in extreme cases, the atrophy, of the gland itself and varies according to whether this makes itself effective in early life or in later life. If the atrophy occurs before birth or in infancy the child becomes a **cretin.** Such individuals may live for many years but when twenty-five or thirty still present a childish appearance. "Stunted, pot-bellied and ugly, they have

TABLE 34:1. THE ENDOCRINE SECRETIONS

NAME OF GLAND	LOCATION IN BODY	PARTS OF GLAND	INTERNAL SECRETION	FUNCTION	EFFECT OF DEFICIENCY	EFFECT OF EXCESS	NECESSARY TO LIFE?
Pancreas	Peritoneal cavity	Islands of Langerhans	Insulin	Control of carbohydrate metabolism	Sugar in urine. Liver loses glycogen	Hunger, weakness	Yes
Intestine	Peritoneal cavity	Mucosa	Secretin	Activates the pancreas to secrete pancreatic juice			?
Adrenal, 7 g	Over kidney	Medulla	Epinephrine or adrenaline or adrenine	Integrates the organism to meet an emergency		High blood pressure	?
		Cortex	Cortin	Regulates water and salt metabolism	Addison's disease, a wasting disease		Yes
Thyroid, 25 g	Neck		Thyroxine	Regulates basal metabolism	Cretinism. Myxedema Goiter (colloid) Obesity (certain types)	Exophthalmic goiter	?
Parathyroid, 1 g	Neck, associated with thyroids		Parathyroid secretion or Parathormone	Regulates calcium metabolism	Tetany, or excessive excitability of nervous system	Softening of bones due to depletion of calcium and phosphorus	Yes
Pituitary 0.65 g	Under side of brain	Anterior lobe	Somatotropic hormone	Growth stimulation	Dwarfism	Gigantism	No
			Gonadotropic hormone	Gonad stimulation	Atrophy of gonads	Overdevelopment of gonads	No
			Thyrotropic hormone	Thyroid stimulation	Atrophy of thyroids	Overdevelopment of thyroids	No
			Adrenotropic hormone	Adrenal stimulation	Atrophy of adrenals	Overdevelopment of adrenals	
			Prolactin	Stimulates breast to produce milk after pregnancy			

TABLE 34:1. THE ENDOCRINE SECRETIONS *(Continued)*

NAME OF GLAND	LOCATION IN BODY	PARTS OF GLAND	INTERNAL SECRETION	FUNCTION	EFFECT OF DEFICIENCY	EFFECT OF EXCESS	NECESSARY TO LIFE?
Pituitary (cont.)		Anterior lobe (cont.)	Diabetogenic hormone	Regulates utilization of carbohydrates and fats			
			Ketogenic hormone	Influences fat metabolism			
		Intermediate lobe	Intermedin	Causes expansion of melanophore in frog. Affects metabolism in man			
		Posterior lobe	Pitressin	Regulates the water content of the body and blood pressure	Obesity Excessive amounts of urine		No
			Pitocin or Oxytocin	Stimulates smooth muscle			
Ovary *	Pelvis	Follicular cells	Oestrin	Promotes development of female secondary sexual characters during puberty. After puberty stimulates enlargement of uterus	Lack of development of secondary sexual characters		No
		Corpus luteum	Progestin	Causes swelling of the mucous lining of the uterus			No
Testis *	Scrotum	Interstitial cells	Testicular hormone	Promotes development of male secondary sexual characters	Lack of development of male secondary sexual characters. Eunuchism		No

* For the hormones of the reproductive organs see Chap. 35.

the intelligence of children of four or five." In not too severe cases deficiency of the thyroid may be corrected by the feeding of thyroxine or the fresh thyroids of such an animal as the sheep. Deficiency of the thyroid in later life gives rise to the condition known as **myxedema,** a disease characterized by a blunting of the mental activities and swellings under the skin, together with a decreased metabolic rate. The third condition is due to overfunction of the thyroid leading to an excess of thyroxine in the blood. This gives rise to the disease known as **exophthalmic goiter,** in which there is an increased metabolic rate associated with nervousness and a pronounced protrusion of the eyes.

4. THE PARATHYROID GLANDS

The parathyroid glands (Fig. 34:1) consist of four small bodies situated in pairs on either side of the thyroid gland or actually imbedded in its substance. The hormone which they secrete, called **parathormone,** has been obtained in extract only. It has been shown to regulate calcium metabolism by controlling the calcium content of the blood. Removal of the parathyroid glands causes an excessive excitability of the nervous system with violent muscular contractions, called **tetany,** which can be corrected by injections of the extract of the gland. When the extract is administered to normal animals softening of the bones occurs due to calcium passing from them into the blood and being excreted.

5. THE PITUITARY BODY

In man the **pituitary** (Fig. 34:1) is a small gland about the size and shape of a pea situated almost exactly in the center of the head. It is suspended from the infundibulum on the under side of the brain by a stalk and lies in a recess in one of the bones forming the floor of the cranium. It consists of three parts called respectively the **anterior, intermediate,** and **posterior lobes.** The pituitary has been named the "master gland" because of the control which it exerts over the other glands of internal secretion. Seven different hormones are claimed for the anterior lobe, one for the intermediate lobe, and two for the posterior lobe.

The hormones of the anterior lobe fall into two groups: one group controlling the growth of the body as a whole or the growth of other endocrine glands, the other group controlling metabolic processes. To the first group belong the somatotropic, gonadotropic, thyrotropic, and adrenotropic hormones. To the second group belong the lactogenic, diabetogenic, and ketogenic hormones. The **somatotropic,** or growth-stimulating hormone, when produced in more than normal amounts causes gigantism, when produced in less than normal amounts, dwarfism. The **gonadotropic** or gonad-stimulating hormone regulates the growth of the ovaries in the female and the testes in the male and will be referred to in Chap. 35, Reproduction. The **thyrotropic,** or thyroid-stimulating, and the **adrenotropic,** or adrenal-stimulating, hormones regulate the growth of these glands. In excess they cause overactivity of the glands with the corresponding effects. Their deficiency causes underactivity of the glands. The lactogenic hormone, called also **prolactin** (L. *lac, lactis,* milk), promotes the growth of the mammary glands during the later part of childbearing and the secretion of milk by the glands immediately after the child is born. The **diabetogenic** hormone aids in regulating the utilization of carbohydrates and fats. The **ketogenic** hormone influences fat metabolism and may be identical with the diabetogenic hormone.

The hormone formed by the intermediate lobe is called **intermedin.** In frogs this hormone causes the expansion of the melanophores, cells in the skin which contain a black pigment. These cells are responsible for the change in color in frogs, which become light colored when placed against a light background and dark colored when placed against a dark background. Frogs from which the pituitary gland has been removed remain light in color even when placed against a dark background. When injected with extracts of the pituitary they become very dark even when kept in light surroundings. In mammals a hormone which appears to be identical with intermedin when injected produces effects similar to those produced by the diabetogenic and ketogenic hormones of the anterior lobe. Two different hormones are recognized in the posterior lobe. One of these, called **pitressin,** regulates the water content of the body and blood pressure; the other, called **pitocin** or **oxytocin,** stimulates the smooth muscles to contract.

6. OTHER ENDOCRINE ORGANS

The endocrine functions of the reproductive organs will be considered in Chap. 35, Reproduction. The thymus gland forms two large masses over the heart which develop rapidly during childhood and after puberty regress so that little trace of them remains in the adult. It is, however, doubtful whether the thymus gland has an endocrine function. The pineal body attached to the roof of the brain is another case of an organ which has been assigned an endocrine function, but so far has not been proved to have one, although recent accurate work suggests a maturin effect on the body.

7. THE INTERACTION OF THE ENDOCRINE GLANDS

The endocrine organs and their secretions constitute a delicatel balanced and complex regulatory mechanism. Although in the abov discussion separate and definite functions have been assigned to th different glands, probably no gland ever acts alone to produce a singl effect; any change in its functioning affects other glands which in tur affect still other glands so that the whole mechanism becomes changed.

Topical Outline of Chapter 34

1. The pancreas 651
2. Adrenal glands 652
3. The thyroid gland 653
4. The parathyroid glands 656
5. The pituitary body 656
6. Other endocrine organs 657
7. The interaction of the endocrine glands 658

Questions

1. What is a hormone? Illustrate your answer with an example.
2. Where is insulin formed? What is its function in the body? What is known regarding its chemical composition?
3. Where is adrenaline formed? What is its chemical formula? What effect does it produce on the body?
4. Name the secretion of the thyroid. What is the chemical composition of the secretion? Discuss the effects of deficiency and excess of the secretion.
5. Where are the parathyroid glands? Are they necessary to life?
6. Name the secretions of the anterior lobe of the pituitary gland and discuss the effects of their deficiency and excess.

Suggestion for Further Reading

Hoskins, R. G., *The Tides of Life, the Endocrine Glands in Bodily Adjustment*, W. W. Norton & Company, Inc., New York, 1933.

CHAPTER 35

Reproduction

I. IN THE FROG

The **testes** of the frog are two small, white, sausage-shaped bodies which lie in the body cavity one on the ventral side of each kidney and are attached to it by a thin supporting membrane called the **mesorchium** (Fig. 35:1). The interior of a testis consists of numerous fine tubules ined by a cellular membrane. Certain of the cells in this membrane give rise to spermatozoa by a process called **spermatogenesis** which will be described in a later chapter. The spermatozoa when formed pass into he cavities of the tubules. The tubules lead into a number of small ducts called **vasa efferentia** which pass from the testis through the meorchium to the kidney where they connect with the **collecting tubules.** The spermatozoa pass through the collecting tubules to the ureter and hrough it to the cloaca and to the exterior. In many species of frogs the ureter is dilated to form a **seminal vesicle,** but in our common American species, *Rana pipiens*, this is not the case.

The **ovaries** of the frog lie in the abdominal cavity ventral to the kidneys, corresponding in number and position to the testes. At the beginning of the breeding season, which occurs in the spring, they are arge irregular masses which almost completely fill the body cavity and the innumerable small black and white eggs which they contain give to the organ a speckled appearance. The eggs are liberated from the ovaries into the body cavity. From the body cavity the eggs pass through funnel-shaped openings into the **oviducts.** The oviducts are ong, coiled tubes with thick, glandular walls which secrete a gelatinous material with which the eggs become surrounded as they pass through. The posterior end of each oviduct is continuous with a thin-walled, distensible tube, the **uterus,** which opens close to its fellow of the opposite side into the cloaca. When the eggs are laid the gelatinous material with which they are surrounded absorbs large quantities of water so that they become distributed in a mass of jelly. This mass of jelly is usually foun attached to twigs or other objects in the water.

In most temperate countries the breeding season occurs in the spring At this time frogs congregate in the shallow water of ponds and marshe and in the male the clasping instinct becomes dominant over all othe instincts. The male clasps the female with his fore legs just behind he fore legs and hangs tightly, maintaining his hold until she lays her eggs So strong is the clasping reflex that the body of the male may be severe in the middle and the fore part still maintain its hold on the female fo hours.

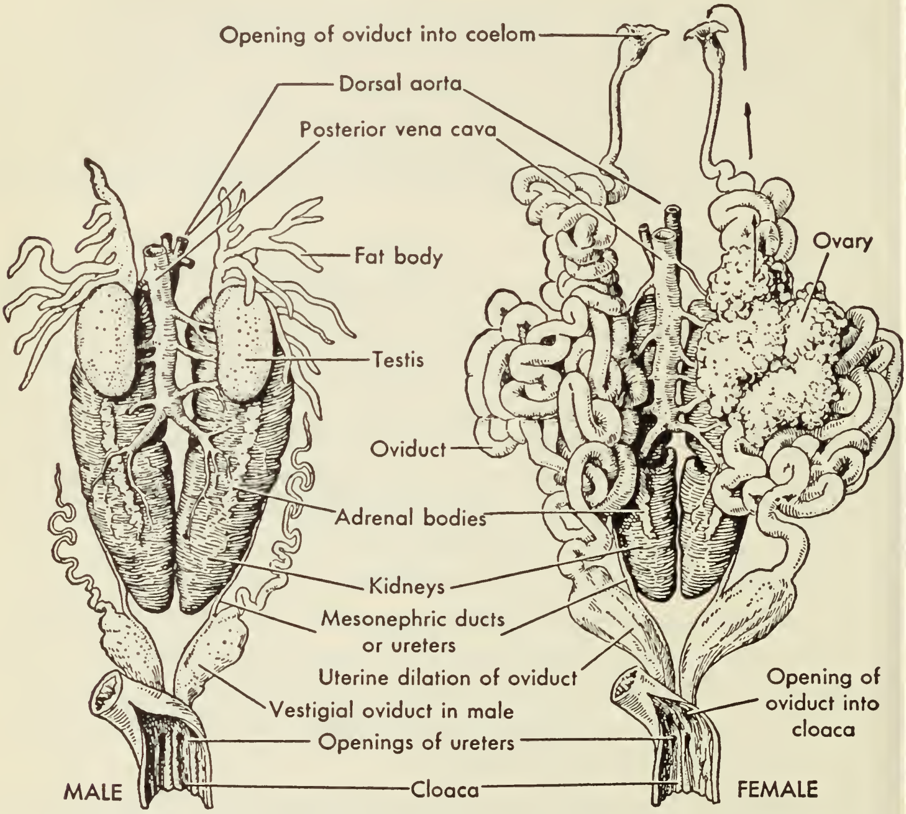
Opening of oviduct into coelom
Dorsal aorta
Posterior vena cava
Fat body
Ovary
Testis
Oviduct
Adrenal bodies
Kidneys
Mesonephric ducts or ureters
Uterine dilation of oviduct
Opening of oviduct into cloaca
Vestigial oviduct in male
Openings of ureters
MALE
Cloaca
FEMALE

Fig. 35:1 The reproductive organs of the frog. From L. L. Woodruff, *Animal Biology* The Macmillan Company.

Usually the eggs are laid only after the male has clasped the femal for several days. Previous to laying, the eggs collect in the two uter which become enormously distended. When the eggs are about to b laid the pair sink to the bottom of the pond and as the female passes he eggs into the water, the male discharges his sperm over them, the spermatozoa penetrating through the jelly to the eggs and fertilizing them

After the male has discharged his spermatozoa the clasping reflex disappears, the pair separates, and the frogs scatter, each to lead his own solitary life until the next breeding season.

The **development** of the frog's egg will be considered in detail in a later chapter; it will suffice for the present to outline the life history. The egg develops into a fishlike creature called a **tadpole** or "polliwog," with a long tail and a large head. The tadpole is a larva and after a certain period metamorphoses into a frog. The metamorphosis consists of the loss of the tail, the development of fore and hind legs and of lungs to replace the gills, and of many other less evident changes, which transform the aquatic larva into the semiterrestrial frog.

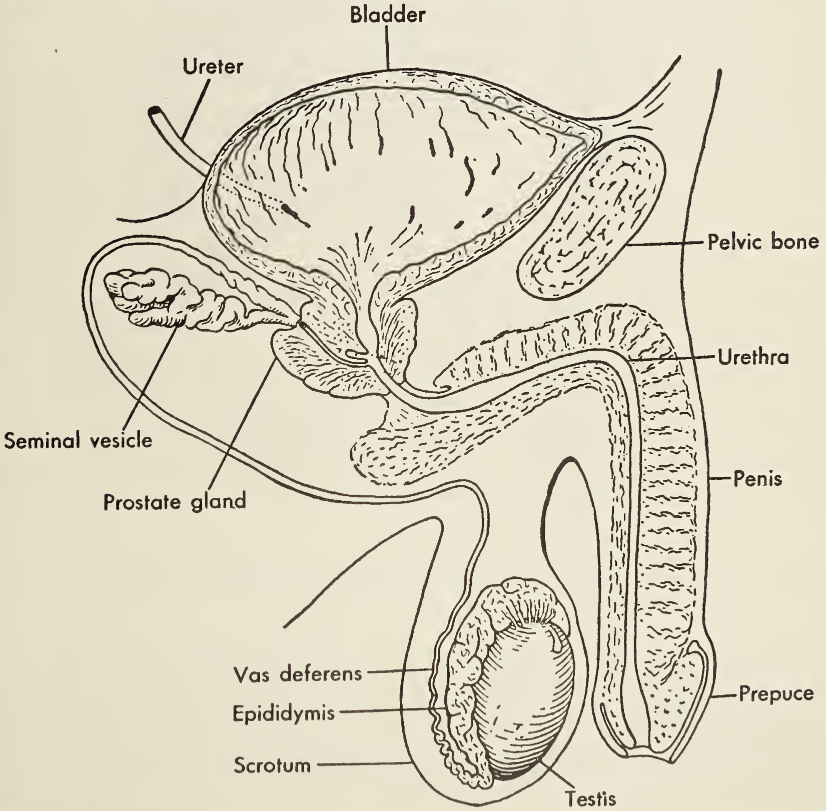

Fig. 35:2 The human male reproductive system. A diagrammatic sagittal section. After Haggard, *The Science of Health and Disease*, by permission of Harper & Brothers.

2. IN MAN

A. MALE REPRODUCTIVE ORGANS

The human **testes** are two small bodies of about the size and shape of a pigeon's egg. They are contained in a sac, the **scrotum,** which hangs from the lower anterior wall of the abdomen (Fig. 35:2). The two separate cavities in the scrotum which the testes come to fill are parts of the coelom and are continuous, in the embryo and in some cases in the adult, with the peritoneal cavity through two short, narrow canals called the **inguinal canals**. The testes undergo their early development in the abdominal cavity in a position corresponding approximately to that which they occupy permanently in the frog and are also connected with the embryonic kidney in a way similar to that in which they are connected in the frog. A short time before birth, or sometimes after birth, each testis descends into the scrotal sac, carrying with it the portion of the embryonic kidney with which it has become involved, and retaining its connections with the sperm duct or vas deferens, blood vessels, and nerves.

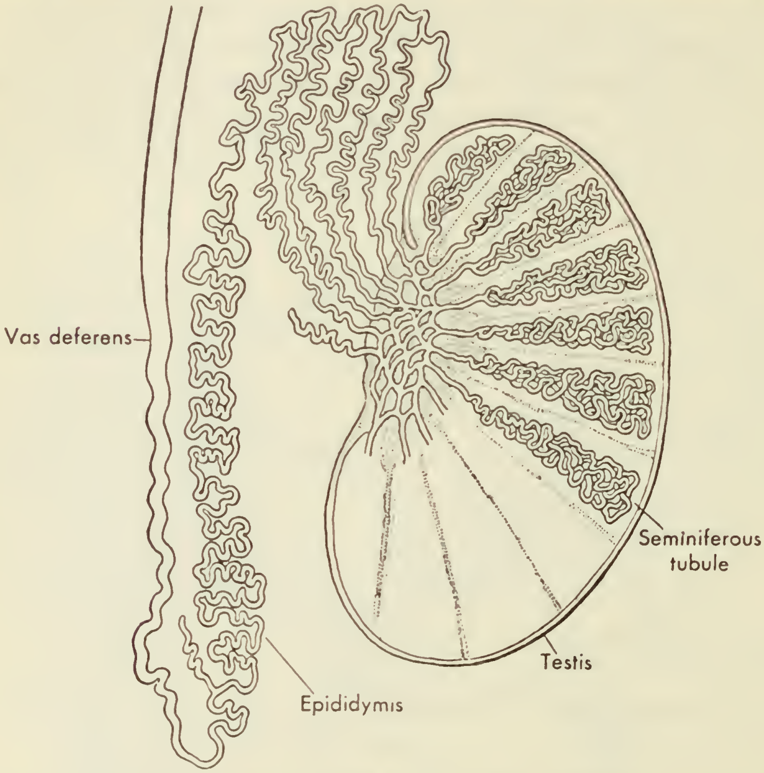

Fig. 35:3 A diagrammatic section of the human testis. After Haggard, *The Science of Health and Disease*, by permission of Harper & Brothers.

The microscopic structure of the human testis (Fig. 35:3) in its main outline is not unlike that of the frog. It consists of numerous coiled **seminiferous tubules.** The portion of the embryonic kidney which moves into the scrotal sac with the testis is converted into the **epidid-**

ymis, a fine tube 20 feet or more in length, but coiled against the testis so as to appear as little more than a bulge on the latter (Fig. 35:2). The end of the epididymis is continuous with the **vas deferens** or sperm duct. Together with the nerves and blood vessels to the testis and a certain amount of supporting tissue, the vas deferens forms the **spermatic cord** which passes from the scrotum through the inguinal canal into the abdominal cavity.

After leaving the inguinal canal the vas deferens curves round on the side wall of the pelvic cavity and passes behind the urinary bladder where it receives the opening of a glandular structure called the **seminal vesicle.** The two seminal vesicles are closely applied to the corresponding ducts and lie between the rectum and the bladder. Beyond the seminal vesicles the vasa deferentia become the **ejaculatory ducts.** These are slender tubes about an inch in length which pass through the **prostate gland** to open into the urethra. The secretion of the prostate gland passes by numerous small ducts into the upper portion of the urethra. The urethra passes through the penis to open at its tip.

B. FEMALE REPRODUCTIVE ORGANS

The human **ovary** is a solid body about the size and shape of a large almond. In the adult it lies against the side wall of the pelvic cavity with which it is connected by folds of the peritoneum (Fig. 35:4). The ovary of a child contains thousands of potential eggs, but only three or four hundred ever reach maturity. Beginning on the average in the fourteenth year, the eggs mature one at a time at intervals of about 28 days. When mature the egg is contained in a **Graafian follicle** which is about as large as a small cherry and bulges from the surface of the ovary. It contains a large amount of liquid and on one side, in a thickening of its wall, is the minute **ovum** or egg cell which is about 0.2 millimeter in diameter. On reaching maturity the follicle ruptures and its contents, including the ovum, are extruded into the body cavity in the vicinity of the opening of the oviduct. The liberation of the egg from the ovary is called **ovulation.**

The opening of each oviduct into the body cavity is enlarged to form a funnel-shaped structure called the **infundibulum,** the irregular, fringed margin of which becomes applied to the ovary and receives the egg. The paired oviducts, called also **Fallopian tubes,** or uterine tubes, open on either side into the single, unpaired **uterus.** The uterus or womb is a hollow, thick-walled, muscular organ, located in the pelvic cavity between the rectum behind and the urinary bladder in front. In shape and size it is not unlike a closed hand, but somewhat smaller. The broad end projects upward into the pelvic cavity while the lower end, which is constricted, projects into the **vagina.** This latter is a slightly curved muscular tube about 3 inches in length. The rounded projection of the uterus into the vagina is called the **cervix** of the uterus. In the young the external opening of the vagina is partly closed by a membrane called the **hymen.** The vagina opens just posterior to the opening of the urethra and the two openings lie in a depression called the **vestibule,** surrounded by two folds of skin called the **inner** and the **outer lips.**

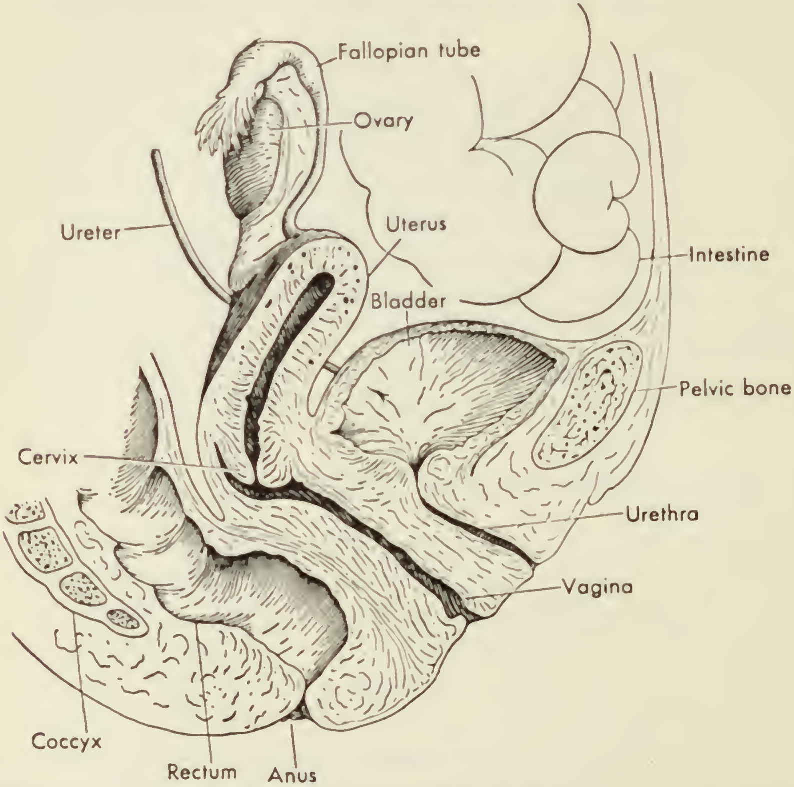

Fig. 35:4 The human female reproductive system. A diagrammatic sagittal section of the pelvis. After Haggard, *The Science of Health and Disease*, by permission of Harper & Brothers.

C. *PUBERTY*

It is usually difficult or impossible to tell whether a newborn baby is a boy or girl from its general bodily characteristics; only in the sexual organs do the sexes differ at this age. As development proceeds differences begin to be noticed until finally rather suddenly the girl begins to take on the form of a woman, and the boy that of a man. In the girl the hips become broad, the breasts prominent, the general contour of the body rounded, and the voice remains high pitched. The boy becomes broad shouldered, his muscles develop, the contour of his body becomes angular, his voice changes to a lower pitch, and he grows a beard. With these structural changes come the changes in temperament and interests which are associated with womanhood and manhood.

These profound changes in body and mind have been shown to be due to the internal secretions of certain of the ductless glands. As already mentioned in the chapter on endocrines, general growth of the body is stimulated by the growth-stimulating hormone of the anterior lobe of the pituitary. The growth and development of the reproductive organs has been shown to be stimulated by the gonad-stimulating hormone, also a secretion of the anterior lobe. In the girl from early childhood on, follicles have been forming round the egg cells in the ovaries. These first follicles do not mature, but after a certain development regress and are absorbed with the eggs which they contain. However, during this partial development, the ovarian follicles form an internal secretion, called **oestrin,**[1] which, passing into the blood, promotes the gradual development of the characteristics which distinguish her. Similarly, the boy, in response to the gonad-stimulating hormone secreted in the anterior lobe of his pituitary, begins to produce in the interstitial cells of his testes, which occupy the spaces between the seminiferous tubules, testicular hormone [2] which stimulates and regulates the development of the characters which distinguish his sex.

Beginning on the average during the fourteenth year and recurring on the average every 28 days, there occurs in girls and women a flow of blood from the vagina called **menstruation**. The flow of blood usually lasts about 3 days. Menstruation continues up to the forty-eighth year on the average when its cessation marks the **menopause** or change of life. However, the ages at which menstruation begins and ends, its regularity, the interval between the periods of bleeding, and the amount of blood vary with the individual, climate, race, and other factors. During this period of 28 days extending from the beginning of one menstrual period to the beginning of the next, the reproductive organs go through a series of changes which constitute the **menstrual cycle.** The blood which gives rise to menstruation comes from the blood vessels of the mucous lining of the uterus, the inner layer of which disintegrates at this time.

[1] Termed also estrone, theelin, folliculin, estrogenic hormone, female hormone.

[2] Termed testosterone, androsterone, androtin, male hormone.

D. OVULATION AND FERTILIZATION

Ovulation, or the liberation of the egg from the ovary, occurs midway between menstrual periods and we may divide the menstrual cycle into three parts: a menstrual period, a preovulatory period, and a postovulatory period. We shall begin our description with the preovulatory period. During this period the mucous lining of the uterus, which became disintegrated during menstruation, is regenerated. At the same time a Graafian follicle in one of the ovaries grows much larger than any of the others (Fig. 37:4). The final rupture of the Graafian follicle gives rise to ovulation. During the days immediately preceding ovulation the secretion of oestrin by the follicle cells of the ovary is especially active and this stimulates growth and enlargement of the uterus. This stimulation of the uterus to growth and enlargement is continued into the postovulatory period due to the large amount of oestrin contained in the follicular fluid which is liberated when Graafian follicles burst. The postovulatory period is characterized by changes in the follicle from which the egg was discharged. This follicle becomes transformed into a mass of yellow tissue called the **corpus luteum.** The corpus luteum forms a hormone called **progestin.** Progestin,[1] like oestrin, acts on the mucous lining of the uterus, but affects especially the inner layer of its mucous lining, causing it to swell and become highly vascular. Thus the uterus is prepared for the egg which passes down the Fallopian tube and arrives there about 4 days after ovulation. If, as most frequently occurs, the egg should not be fertilized, it passes through the uterus and is discharged. Some time after this occurs, the inner lining of the uterus, failing to have received the egg, disintegrates, marking the end of the postovulatory period and the beginning of menstruation. During the menstrual period the corpus luteum declines, and the secretion of progestin falls off suddenly.

Copulation in mammals consists of the insertion of the penis into the vagina, and the injection into it of a quantity of fluid called **semen** containing spermatozoa and the secretions of the prostate gland and of the walls of the seminal vesicle. Human spermatozoa are minute thread-like bodies about 0.05 millimeter in length and enlarged at one end into a head which is almost entirely nucleus. Fertilization normally occurs in the Fallopian tubes. Although the spermatozoa are actively motile it seems unlikely that they make their way to the egg under their own power. Recent investigations on animals seem to indicate that the semen is moved forward by contractions in the walls of the uterus and oviducts in a way similar to that in which peristalsis moves the food materials in the intestines. A distinction is made between copulation which refers to the union of the male and female, insemination which means the introduction of sperm from one individual (male) into another individual (female), and fertilization which involves the union of egg and sperm.

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[1] Termed also progesterone, lutin.

E. THE GENERAL ACCOUNT OF THE DEVELOPMENT OF THE EMBRYO AND FOETUS

If the egg is fertilized the menstrual cycle is interrupted and **pregnancy** intervenes. The fertilized egg begins to divide while still in the Fallopian tube. By the time it reaches the uterus it has increased somewhat in size and consists of a single layer of cells called the **trophoblast,** forming a fluid-filled vesicle containing a small mass of cells, the **inner cell mass,** attached to it on the inside. The trophoblast secretes an **enzyme** which digests the cells of the mucous lining of the uterus and literally eats itself into the uterine wall. This entrance of the ovum into the uterine wall is called **implantation.** The irritation of the mucous membrane caused by the implantation of the ovum stimulates the uterus to further growth and leads to the formation of the placenta.

The **placenta** begins to develop immediately after the implantation of the ovum. This structure, which establishes the connection between the mother and child and furnishes the means of transfer of food materials and waste products, is formed partly from tissue developed from the egg and partly from the wall of the uterus (Fig. 36:17). The two tissues become closely applied to each other but there is never any continuity between the blood vessels of the mother and the blood vessels of the embryo, which develops its own blood and blood cells. There is also never any nervous connection between the two organisms. The transfer of food substances and waste products and the exchange of gases occur by diffusion through the walls of the blood vessels. This state of affairs is often a fortunate one for the developing child since the germs of nearly all infectious diseases are unable to pass from the mother to the child.

The embryo develops from the embryonic cell mass within the trophoblast. It lies in a fluid-filled cavity called the **amniotic cavity** surrounded by the placenta with which it is connected only by a long, usually coiled cord, the **umbilical cord** (Fig. 35:5). In this cord, which is developed from the egg, are the two arteries and vein which pass from the embryo to that portion of the placenta which is also developed from the egg. During the first 6 weeks of its prenatal life, the new individual is called an **embryo.** From that time until birth it is called a **foetus.** The growth of the embryo is gradual, an embryo at the end of the first month measuring about 7.5 millimeters or 3/10 inch in length; one at the end of the first 6 weeks, about 17 millimeters or 2/3 inch. The growth of the foetus is more gradual, its length at the end of 2 months being 30 millimeters, 3 months, 7 centimeters, 4 months, 13 centimeters, 5 months, 20 centimeters (25 centimeters or 1 foot if the legs are included). At birth, which usually occurs at the end of 10 lunar months or 9 calendar months, the average length is 50 centimeters or 20 inches.

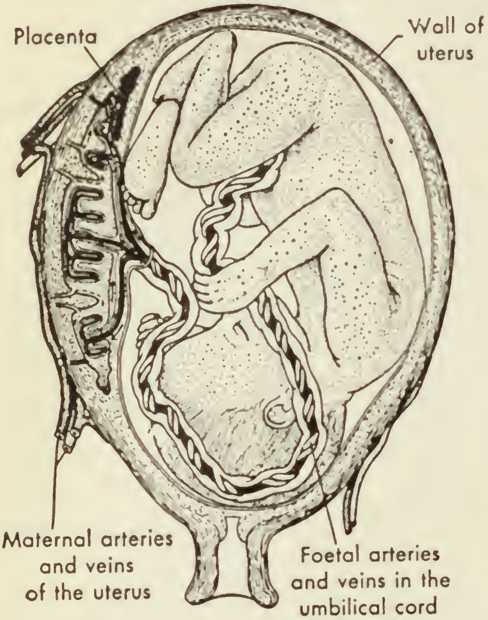
Placenta
Wall of uterus
Maternal arteries and veins of the uterus
Foetal arteries and veins in the umbilical cord

Fig. 35:5 A uterus containing an advanced foetus attached to the placenta by the umbilical cord. From T. I. Storer, *General Zoology,* McGraw-Hill Book Company, Inc.

With the progress of pregnancy many changes occur in the mother, most if not all of which are initiated and controlled by internal secretions, the exact nature and source of which are, however, unknown. Ovulation and menstruation cease immediately and are not resumed until after the child is born. The breasts become enlarged in preparation for the secretion of milk. Sudden cessation of menstruation is usually considered a sign of pregnancy. A more reliable test has been recently developed. It has been found that the urine of pregnant women contains large quantities of the gonad-stimulating hormone of the anterior pituitary. Injection of this into a mature female rabbit causes ovulation and it is only necessary to etherize and surgically examine the animal's ovaries 16 hours later to determine whether the urine injected was that of a pregnant or nonpregnant woman.

At the end of pregnancy the foetus lies in a fluid-filled cavity bounded by the placenta. The beginning of childbirth is characterized by contractions of the smooth muscles of the uterus. These contractions give rise to the pains of "labor" which last until the child is born. The muscles of the uterus are said to be stimulated to contract by a hormone called **oxytocin** produced by the pituitary. These contractions gradually increase in strength and after several hours the child is forced into and through the birth canal. The birth canal is in reality the vagina distended to coincide with the opening of the pelvis, which has already been referred to in considering the skeleton. In most cases when the child is born the placenta is left in place in the uterus and the umbilical cord which becomes uncoiled extends from the newborn child to the placenta. While the umbilical cord is intact and the placenta in place the child continues to depend on its mother for its respiration. To free the child from its mother, the umbilical cord is first tied to prevent the child from bleeding to death and then cut on the side toward the mother. When the child is born its lungs are completely collapsed. When the umbilical cord is tied and the child is no longer able to depend on its mother to give it oxygen and take away carbon dioxide, the carbon dioxide accumulates in its blood. This stimulates its respiratory center in the medulla, and the inspiratory muscles of its chest and diaphragm contract filling its lungs with air. Soon after the child is born the placenta is expelled from the uterus as the "afterbirth." Its separation from the wall of the uterus occurs in the vascular portion of the maternal mucous membrane and the mother is prevented from bleeding to death by the continued contractions of the uterine muscles. Childbirth has always been regarded as a very serious experience for both the mother and the child; both must immediately adjust themselves to greatly changed conditions, the mother to the passage of the child from her body and the sudden lifting of the burden of providing for the infant's nourishment and excretion; the child to the passing from a truly parasitic and aquatic life in a liquid medium to a relatively independent life in the air.

Topical Outline of Chapter 35

1. In the frog 659
2. In man 661
    A. Male reproductive organs 661
    B. Female reproductive organs 663
    C. Puberty 664
    D. Ovulation and fertilization 666
    E. The general account of the development of the embryo and foetus 667

Questions

1. Describe the breeding activities of the frog.
2. In the frog trace the path of a sperm from its point of origin until its fusion with an egg.

3. In the frog trace the path followed by an egg from its point of origin until it arrives in the water.
4. Describe the male reproductive organs in man and trace the path followed by the sperm.
5. Describe the female reproductive organs in man. Where does fertilization occur?
6. Describe the changes which occur in the male and female at puberty.
7. Discuss the relation of ovulation to menstruation and the development of the corpus luteum.
8. Describe briefly the development of the human embryo and foetus.
9. Describe the sequence of events in childbirth.

Suggestion for Further Reading

Parhsley, H. M., *The Science of Human Reproduction*, W. W. Norton & Company, New York, 1933.

PART V. Development and Heredity

"Every animal appears as a sum of living units, each of which bears in itself the complete characteristics of life."

Virchow

CHAPTER 36

The Development of the Individual (Embryology)

1. THE ORIGIN OF THE INDIVIDUAL

We have already seen that both animals and plants reproduce by two fundamentally different methods. In **asexual** reproduction, a part of the parent (in this case there is only one parent) is separated and grows into a new individual. In **sexual** reproduction there is a fusion of two gametes, an egg and a sperm, which usually come from different parents, and the new individual which develops from the fertilized egg contains materials from both parents. Thus in sexual reproduction the new individual is "new" in the sense that it usually contains new potentialities derived from the mixture of materials from the two individuals. The study of development or embryology concerns itself with the development of the fertilized egg, the product of sexual reproduction. The processes (spermatogenesis and oögenesis) which lead up to and prepare the egg and sperm to unite in fertilization will be described in a later chapter. We will pass at this time to a consideration of the mature gametes.

2. THE SPERMATOZOON AND THE OVUM

The spermatozoa of animals differ in size and details of structure but nearly all agree in possessing a **head** which is composed almost entirely of nuclear matter, a long flagellum called the **tail,** and connecting these two a **middle piece** which contains the centrosome of the cell (Figs. 36:1 and 36:2). In all animals the sperm requires a liquid medium for its existence and for its union with the egg. Fertilization must therefore always occur in the water as in aquatic forms or in specially constructed capsules (earthworm), or within the body of the female (insects, vertebrates, and most land animals).

The mature egg is usually a more or less spherical cell surrounded by a resistant noncellular covering, the **vitelline membrane.** However, the eggs of animals differ greatly in size and structure and surrounding membranes, the differences consisting chiefly of adaptations to different methods of development. There is some doubt regarding a vitelline membrane in mammals and man, its place being to some extent taken by the **zona pellucida** formed by the follicle cells which surrounded the egg in the ovary. Food material in the form of yolk is stored in the cytoplasm of the egg for the use of the embryo during its development, and the amount of this yolk to a great extent determines the size of the egg. In those animals in which the embryo reaches at an early stage a condition in which it is able to procure its own food (most invertebrates),

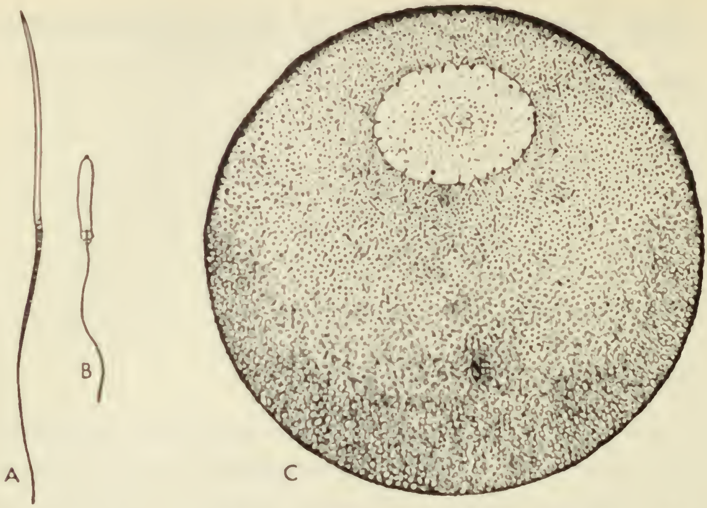

Fig. 36:1 Egg and spermatozoa of frog. A, spermatozoön of *Rana fusca.* After Broman. B, spermatozoön of *Rana esculenta.* After Broman. C, section through the fully formed ovarian egg of a frog. From Morgan, *Development of the Frog's Egg*, The Macmillan Company. The animal pole is covered with a thin layer of pigment and the vegetal pole is filled with yolk bodies. The large nucleus, or germinal vesicle, surrounded by a definite nuclear membrane, lies eccentrically toward the animal pole. From Kellicott, *Outlines of Chordate Development*, by permission of Henry Holt and Company, Inc.

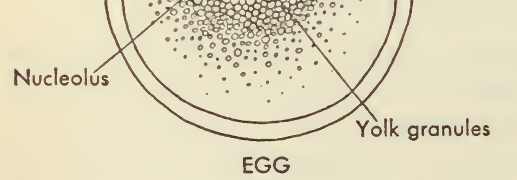

Fig. 36:2 A human egg cell and a sperm drawn to the same scale. The actual diameter of the human egg is approximately 0.2 millimeter.

or in which food is provided for it by the mother (placental mammals), the egg contains little yolk and is relatively small. When, on the other hand, as is conspicuously the case in reptiles and birds, the embryo develops to an advanced stage while still within the egg, a great amount of yolk is stored and the egg is large. Thus all sizes of egg cells occur from the minute microscopic ova of hydra or man to the relatively enormous cell represented by the "yolk" of the "egg" of an ostrich. Additional food material may be placed about the egg outside the vitelline membrane as in the case of the jelly which covers the frog's egg or the albumen of the hen's egg which is formed as the "yolk" passes down the oviduct. Eggs which are laid on land and undergo their developemnt there are usually provided with **shells,** which protect them from mechanical injury and from loss of moisture. Such shells may be formed of chitin as in insect eggs, of horny material as in reptile eggs, or of calcareous material as in the eggs of birds.

The most important contributions of the sperm and egg to the zygote are listed in Table 36:1.

TABLE 36:1. CONTRIBUTIONS OF THE SPERM AND EGG TO THE ZYGOTE

SPERM CONTRIBUTES	EGG CONTRIBUTES
Chromosomes	Chromosomes
Centrosome	Vitelline membrane
	Cytoplasm
	Yolk

3. THE EARLY DEVELOPMENT OF THE STARFISH

The early cell divisions of the fertilized egg, called **cleavage,** depend to a considerable extent on the amount of yolk and the location of the nucleus with reference to the yolk in the egg. The division of the cells is, of course, always preceded by the mitotic division of the nuclei. We will begin the study of embryology with the egg of the starfish (Fig. 36:3) since it has a comparatively small amount of yolk and undergoes in its early stages what is believed to be a relatively simple development.

At its **first cleavage** the small spherical egg divides by cell division into two equal hemispherical cells, giving rise to a **two-celled stage.** At the **second cleavage** each of these cells divides, giving rise to a **four-celled stage,** the plane of division being at right angles to the first. The first two planes of division may be said to be meridional with reference to the spherical egg and its poles. The **third cleavage** is in an equatorial plane at right angles to the first two and gives rise to an **eight-celled stage.** In the **fourth cleavage,** which leads to the **sixteen-celled** stage, the planes of cleavage are again meridional. Cell division proceeds with more or less regularity until there results a ball of cells surrounding a cavity. This stage is called a **blastula** and the cavity which it contains a **blastocoel.** The resemblance of the blastula stage of the starfish egg to a volvox colony should be noted.

Although the cells of the blastula form an almost perfect sphere and are nearly all equal in size, the cells at one pole, called the **animal pole,** are somewhat smaller than the cells at the other pole, the **vegetal pole.** As cell division continues the vegetal pole becomes flattened and eventually invaginated into the blastocoel, much as one might push in one side of a soft, hollow, rubber ball. The blastula then becomes a **gastrula.** The invaginated cells become the **endoderm** and surround a new cavity, the **enteron,** which opens to the exterior at the region of invagination by an opening called the **blastopore.** The outer cells form the **ectoderm** which at this stage is ciliated. Thus in the gastrula the cells are differentiated into two embryonic layers, or **germ layers.** In many respects the gastrula stage of the starfish has the characteristics of a simplified coelenterate. Indeed if we imagine hydra devoid of its tentacles and contracted, as it sometimes is, into a small sphere it would closely resemble a gastrula. It should be noted that the cells of the hydra show a much greater structural differentiation than those of the gastrula and are in fact fully differentiated cells, while the cells of the gastrula are embryonic cells which have yet to undergo differentiation and specialization.

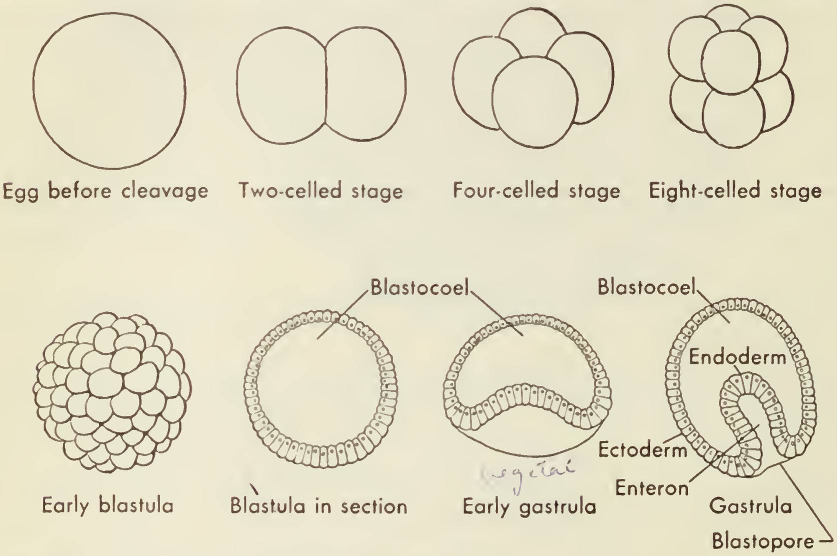

Fig. 36:3 The early development of the starfish.

As the development proceeds, from the inner end of the enteron two pouches grow out into the blastocoel. Later these pouches become separated from the enteron and their cavities become a part of the coelom of the starfish. During this development the blastopore becomes the anus and the mouth is developed as a new opening between the enteron and the exterior. The gastrula develops into a larva which swims about and later settles to the bottom and changes into a starfish.

4. THE DEVELOPMENT OF THE FROG

A. CLEAVAGE AND GASTRULATION

The egg of the frog is about 2 millimeters in diameter and compared with that of the starfish contains a relatively large amount of yolk. The large nucleus is located somewhat toward one pole which is recognized as the **animal pole** and distinguished from the opposite pole which is called the **vegetal pole.** Usually as the eggs float in the water the animal pole is uppermost. The upper hemisphere containing the animal pole is dark in color due to a layer of brown pigment which lies just under the vitelline membrane.

The beginning of the **first cleavage** is marked by a furrow on the surface of the egg which starts at the animal pole and gradually extends toward the vegetal pole dividing the egg into **two cells** (Fig. 36:4). This division, which since it passes from pole to pole may be called **meridional,** is followed by a second meridional division at right angles to the first which also begins at the animal pole. The result of this second cleavage is the **four-celled stage.** The third cleavage is parallel to, but somewhat above, the equator of the egg, so that in the **eight-celled stage** the four cells at the animal pole are somewhat smaller than the four at the vegetal pole. The planes of the divisions which result in the **sixteen-celled stage** are again meridional and begin at the animal pole, so that the eight smaller cells which are formed at this pole appear before the eight larger cells formed at the vegetal pole. The cell divisions which lead to the **thirty-two-celled stage** are parallel to the equator of the egg but do not occur simultaneously, the divisions above the equator occurring before those below the equator. At or about this stage the divisions usually become irregular so that it is quite unusual to see an egg with exactly sixty-four cells. As development proceeds the cell divisions become more rapid and more frequent at the animal pole so that the **blastula stage** consists of a ball of cells which are smallest at the animal pole but gradually increase in size toward the vegetal pole. The relative size of the cells is expressed internally as well as externally so that the blastocoel is nearer to the animal than the vegetal pole.

Like the starfish egg the frog's egg passes through a **gastrula stage.** However, the inequality in size of the cells and the great amount of yolk introduces certain differences, one might almost say certain difficulties, in the process of gastrulation. The large yolk-laden cells of the vegetal pole, called also **yolk cells,** seem on account of their relatively lesser content of living substance unable to move inward as do the cells of the starfish egg. Instead the small cells of the animal pole, which are dark because of the pigment they contain, grow over the larger light-colored yolk cells toward the vegetal pole. The margin of this overgrowth grows downward over the yolk cells, gradually enclosing them until only a light circular area called the **yolk plug** is visible.

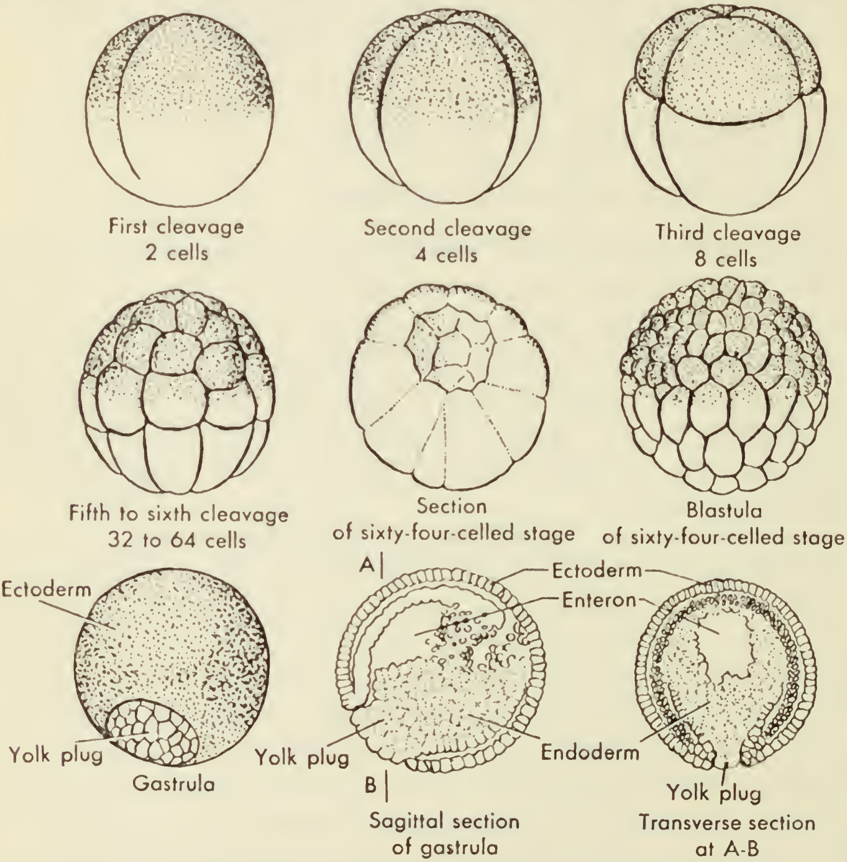

Fig. 36:4 The development of the frog from the egg to the gastrula stage.

When the gastrula of the frog is compared with that of the starfish it is easily seen that the circular area which is occupied by the yolk plug corresponds to the blastopore of the starfish egg. As the development proceeds the egg rotates in the jelly and the yolk plug moves upward and comes to occupy a position which the subsequent development shows to be the posterior end of the embryo. A vertical section cut from animal to vegetal poles and through the yolk plug (Fig. 36:4) indicates that there is an ingrowth of small cells from the margin of the blastopore which is most active in the upper or dorsal region. This ingrowth is in reality an invagination and leads to the formation of a cavity, the **enteron.** In the frog the enteron bursts through into the blastocoel so that the two cavities become continuous. The small outer pigmented cells become the **ectoderm,** the small cells which grow in from the rim of the blastopore together with the yolk cells form the **endoderm.**

After the process of gastrulation is well under way, the formation of the **mesoderm** and the **notochord** begins. The cells from which these arise grow in from the rim of the blastopore where ectoderm and endoderm meet and grow inward and anteriorly between the ectoderm and endoderm. The cells which grow inward from the sides of the blastopore rim form mesoderm, those which grow inward from the dorsal part of the rim and come to extend through the entire middorsal region, form the notochord. As development proceeds the two sheets of mesoderm extend laterally and ventrally so as to enclose the entire mass of endoderm. In some vertebrates the notochord appears to arise directly from the endoderm, in others from the mesoderm. For the frog a mixed origin has been claimed. For the purposes of this discussion it may be regarded as arising from the dorsal portion of the lip of the blastopore.

B. DEVELOPMENT OF THE TADPOLE

(1) EXTERNAL FEATURES

In a previous section it was stated that the blastopore marked the posterior end of the embryo. With further development the embryo (Fig. 36:5 A) elongates, becoming at the same time thinner in cross section. The anterior end becomes slightly enlarged, forming the head. From the posterior end a tail grows out. Gradually a small tadpole is formed. The young tadpole as it hatches (Figs. 36:6 and 36:8), although elongated, is no larger than the egg from which it developed. There has been little if any growth. The processes which have been going on are cell division and differentiation.

We will not attempt to describe the development of the embryo as a whole, but rather to follow the development of the separate systems. These will be considered in the following order: systems developed primarily from the ectoderm, systems developed primarily from the endoderm, systems developed primarily from the mesoderm. It must be borne in mind, however, that the development of these systems usually goes on simultaneously and the organs of each system usually contain cells from all of the germ layers, although generally the main function of the system is determined by cells from one of the three layers.

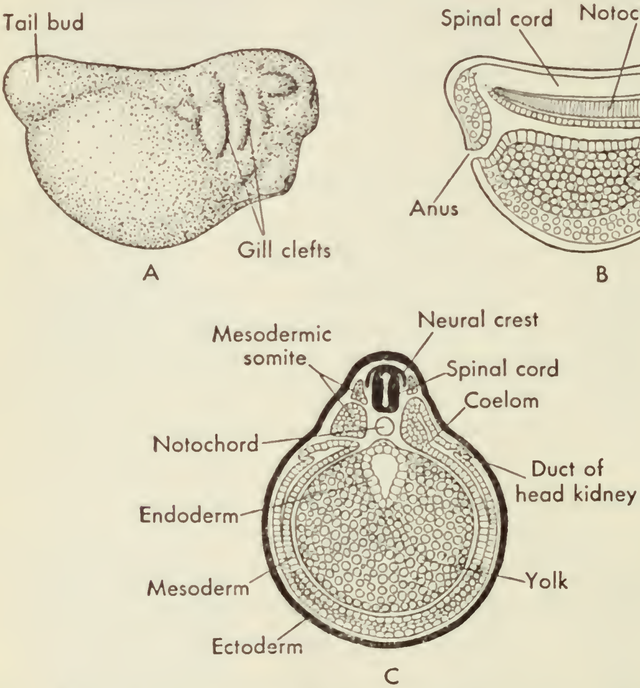

Fig. 36:5 A frog embryo, before hatching, at the beginning of elongation. A, external lateral view. B, sagittal section. C, transverse section. The myomeres are here called mesodermic somites. The pronephros is called the head kidney. After Marshall, *Vertebrate Embryology*, by permission of G. P. Putnam's Sons.

(2) SYSTEMS DEVELOPED PRIMARILY FROM THE ECTODERM

(a) THE SKIN

The skin of the adult is composed of two layers, the epidermis and dermis. The epidermis consists of a few layers of cells of ectodermal origin. The dermis is developed from the mesoderm. The pigment cells and mucous glands are in the dermis.

(b) THE NERVOUS SYSTEM

The nervous system develops as an infolding of the ectoderm in the dorsal region of the embryo. First the ectoderm over this portion becomes thickened and flattened to form a triangular plate, the **neural plate,** extending from the blastopore, where it is narrowest, to the animal pole, where it widens out. The margins of this plate become raised, forming **neural folds,** which extend posteriorly to include the blastopore, and anteriorly over the future head of the embryo. The neural plate gradually sinks down between the folds and these bend over and meet dorsally along the median line. Beginning at about the middle of the embryo and extending to either end, the approximated neural folds fuse together. Thus there is formed a neural tube which extends the entire length of the embryo and is covered with a layer of superficial ectoderm. Since the blastopore is included in the area surrounded by the neural folds it opens into the neural tube when the latter is completed, forming a **neurenteric canal** which, however, later becomes closed. Certain ectodermal cells at the lateral margins of the neural plate do not enter into the formation of the neural tube but remain on either side as separate strands which become segmented into groups of cells called **neural crests** (Fig. 36:5 C) lying dorsally along each side of the neural tube. The anterior portion of the neural tube, which from the beginning is the larger, forms the brain; the posterior portion forms the spinal cord. Early in

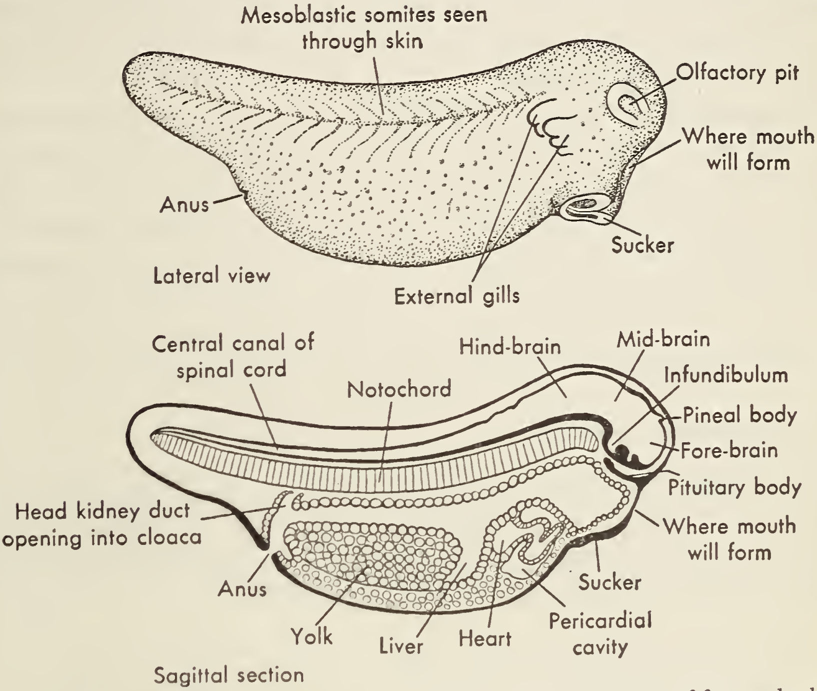

Fig. 36:6 Above, external lateral view and below, sagittal section of frog tadpole just after hatching. The pronephros is here called the head kidney, and the myotomes are called mesoblastic somites. After Marshall, *Vertebrate Embryology*, by permission of G. P. Putnam's Sons.

its development the brain is divided by two constrictions into **fore, mid,** and **hindbrains.** Later the forebrain becomes constricted and divided into the **telencephalon** and **diencephalon,** while the hindbrain becomes similarly divided into the **metencephalon** and **myelencephalon.** The midbrain becomes the **mesencephalon.**

At an early stage (Fig. 36:6) there occurs an ingrowth of the superficial ectoderm of the anterior end just ventral to the forebrain. This ingrowth later becomes associated with the infundibulum and forms the **anterior lobe of the pituitary body.**

The **nerves** of the peripheral nervous system grow out from the neural tube and the neural crests. From the ventral portion of the neural tube motor nerve cells send out processes which thread their way through the tissues to muscles or glands and become the fibers of **motor nerves.** The cells of the neural crests become the ganglion cells of the **dorsal ganglia** of the spinal cord. Processes grow out from these ganglion cells toward the spinal cord, and peripherally to the skin and other parts of the body. The latter processes become the nerve fibers of the **sensory nerves.**

(c) THE SENSE ORGANS

The development of the vertebrate **eye** is peculiar (Fig. 36:7). At an early stage two thickened, pigmented areas called the **optic placodes** appear in the neural plate near its anterior end. As the neural tube is formed the optic placodes become included in the walls of the tube. The cells of the optic placode grow rapidly and at about the time of formation of the forebrain have formed two saclike vesicles called **optic vesicles,** extending out on either side and connected with the forebrain by hollow **optic stalks.** When the outer surfaces of the optic vesicles reach the inner surface of the superficial ectoderm they invaginate so that each optic vesicle becomes converted into a double-walled **optic**

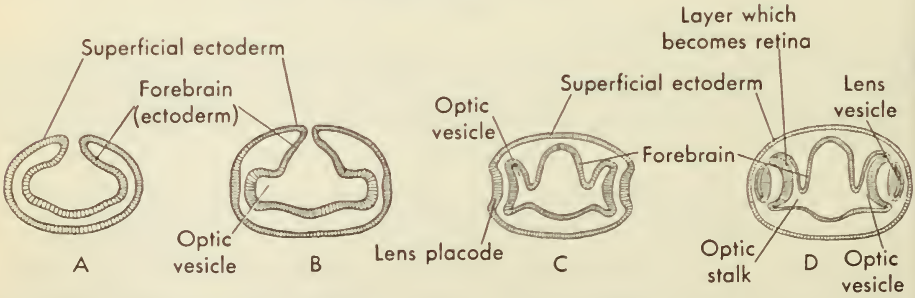

Fig. 36:7 The development of the eye. A, B, C, D, successive stages showing the formation of the optic vesicle and the lens.

cup, the opening of which is turned toward the outer surface of the body. The opening of the cup becomes the pupil and from the rim the iris develops. The cells of the inside layer of the optic cup form the **retina** of the eye (Fig. 36:7 D). From certain of these cells the nerve fibers of the **optic nerve** grow out and pass under the optic stalk to the brain. When the forebrain becomes divided into telencephalon and diencephalon the attachment of the optic stalk and the entrance of the optic nerve are included in the diencephalon.

When the ectoderm, which forms the retina, is followed through its various foldings to the optic cup and its final position in the functional eye, it can be seen that the surface of this ectoderm which was originally on the outside of the embryo becomes reversed so that it is turned toward the interior of the body and away from the light rays which enter through the pupil. Since sensory cells are usually developed on an external surface and send their nerve processes away from the surface we have here a developmental reason for the inversion of the retina.

At about the time the optic vesicle is formed the superficial ectoderm over it becomes thickened to form a **lens placode.** In many vertebrates this placode forms a lens vesicle which later becomes converted into the solid transparent lens. In the frog, however, the lens appears first as a solid mass of cells which then becomes for a time vesicular and later solid. The accessory parts of the eye, such as the choroid and sclerotic coats, blood vessels, and muscles, are developed from mesoderm (mesenchyme).

The inner **ears** begin their development as two thickenings of the superficial ectoderm, called **auditory placodes,** one on each side of the hindbrain. Later each placode becomes invaginated forming an **auditory vesicle,** opening on the surface of the body. The ectoderm of the auditory vesicle becomes the lining of the cavity of the internal ear. In some vertebrates (e.g., dogfish) the connection of the auditory vesicles with the exterior persists. In the frog a part of the canal persists as an endolymphatic duct. In the walls of the auditory vesicle sensory cells develop and become surrounded by the fibers of the auditory nerve. In most vertebrates in which there is a middle ear, it is developed from the endoderm of the first gill cleft.

The **olfactory organs** which form a part of the lining of the nasal cavities are developed from **olfactory placodes,** thickenings of the superficial ectoderm just in front of the neural tube. The placodes invaginate to form **olfactory pits** which become enlarged to form nasal cavities. Certain of the cells of the placode become sensory cells of the olfactory epithelium and send nerve fibers to the brain.

(3) SYSTEMS DEVELOPED PRIMARILY FROM THE ENDODERM

(a) THE DIGESTIVE SYSTEM

We left the enteron as an irregular cavity in the gastrula surrounded by the endoderm. With the growth in length of the embryo this cavity becomes elongated (Fig. 36:6). Quite early a posteriorly directed outpocketing of the anterior region marks the beginning of the formation of the **liver.** At the posterior end of the embryo the endoderm forms an outgrowth toward the exterior and the superficial ectoderm forms a corresponding ingrowth called the **proctodaeum.** Where the ectoderm and endoderm meet a passageway is established. The proctodaeum forms a portion of the lining of the future **cloaca,** the rest of the lining of the cloaca being formed of endoderm. The actual opening of the proctodaeum to the exterior is called the **anus.**

At a later stage an invagination of the superficial ectoderm at the head end of the embryo, just ventral to the brain, forms the **stomodaeum.** The endoderm grows out against the ectoderm of the stomodaeum and eventually, about the time the tadpole hatches, the thin partition is broken through. The greater part of the epithelial lining of the **mouth cavity** is formed from the stomodaeum. The differentiation of the different parts of the digestive tube into pharynx, esophagus, stomach, and intestine occurs gradually. Only the epithelial lining or mucosa is formed from the endoderm. The invagination which marked the beginning of the liver grows out and, ramifying, gives rise to a tangled mass of tubes. From the main tube and its immediate branches develop the bile ducts and the gall bladder. The cells lining the finer branches become the liver cells which secrete the bile. The development of the pancreas is similar to that of the liver.

(b) THE RESPIRATORY SYSTEM

The **gill clefts** first appear as solid outgrowths from that portion of the endoderm which will eventually form the lining of the pharynx. These outgrowths grow toward and come into contact with the superficial ectoderm. Later, in each of these outgrowths, **gill pouches** are formed so that, in all, six pairs of gill pouches are formed on each side. The first pair of these are called the **hyomandibular pouches,** the next five are named in order, the first, second, third, fourth, and fifth **branchial pouches.** At about the time of hatching the first four branchial pouches become gill clefts by the fusion of the endoderm with the superficial ectoderm and the formation of a gill slit (Fig. 36:8), thus placing the pharynx in communication with the exterior through the gill clefts. In the frog the hyomandibular pouch does not become a cleft and disappears when the other pouches open to the exterior.

The solid masses of tissue anterior and posterior to the gill pouches or clefts are called **gill arches.** The pair in front of the hyomandibular pouches are called the **mandibular arches;** from them the lower jaw or mandible is later developed. The pair of arches anterior to the first branchial pouches are called the **hyoid arches,** the next four are named in order, the first, second, third, and fourth branchial arches.

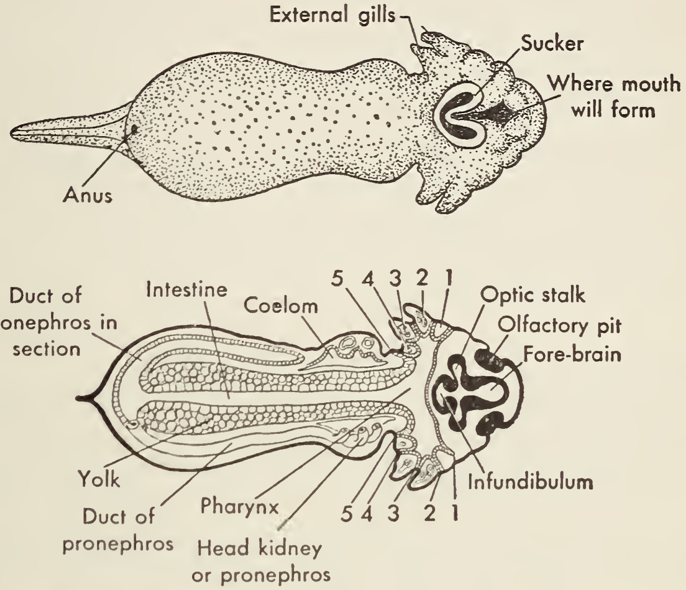

Fig. 36:8 Above, an external ventral view of a frog tadpole just after hatching. Below, a frontal section of a frog tadpole in the same stage. In the numbered figure, 1 to 5 (upper) are gill arches, 1 being the hyoid arch and 2 to 5 being the first four branchial arches, while 1 to 5 (lower) are gill pouches, 1 being the hyomandibular pouch and 2 to 5 being the first four branchial pouches. The mandibular arch, which is not labeled, is in front of the hyomandibular pouch. After A. M. Marshall, *Vertebrate Embryology*, by permission of G. P. Putnam's Sons.

In most vertebrates (apparently the frog is an exception) the hyomandibular pouch gives rise to the middle ear. The tympanum develops where the endoderm of the pouch meets the superficial ectoderm. The Eustachian tube develops from the portion of the pouch nearest the enteron, and thus places the cavity of the middle ear in communication with the pharynx.

In the newly hatched frog tadpole the function of respiration is carried on by three pairs of **external gills** which develop as outgrowths from the superficial ectoderm of the first, second, and third branchial arches. Later, at about the time the mouth opening appears, **internal**

gills are developed from the endodermal walls of the gill clefts and the external gills disappear. The gill clefts, gill arches, and internal gills are regarded as being homologous to the similar organs in fishes.

At about the time of disappearance of the external gills a fold of ectoderm arises in front of the first gill cleft and grows backward, covering the other clefts and fusing with the body behind the last pair of clefts so as to form a cavity surrounding the gill clefts and the portion of the body ventral to them and communicating with the exterior by a single opening on the left side. This ectodermal fold is called the **operculum.** The gills disappear at metamorphosis and the frog then breathes with its lungs.

The lungs first appear before hatching as a pair of small outpocketings from the ventral wall of the portion of the enteron which becomes the esophagus. With the approach of metamorphosis they increase in size and the endoderm around their openings into the enteron becomes constricted off to form the larynx.

(4) SYSTEMS DEVELOPED FROM THE MESODERM

We left the mesoderm as two sheets of tissue, one on either side of the endoderm extending from the notochord to the ventral side of the embryo. Soon after this, each of the layers splits into two layers between which a cavity, the future **coelom,** appears. On each side of the embryo the mesoderm becomes separated by a horizontal longitudinal division into dorsal and ventral portions (Fig. 36:5 C). The dorsal portion, called the **vertebral plate,** becomes divided transversely into a series of **myotomes** or muscle segments, while the ventral portion, called the **lateral plate,** remains unsegmented. The myotomes are a conspicuous feature in a lateral view of a newly hatched tadpole. The cells of the myotomes elongate and develop into the fibers of the voluntary muscles of the body. At the beginning of their development the myotomes contain a portion of the coelom. This, however, soon disappears. The outer layer of the lateral plate, called the **somatic layer,** comes to lie under the superficial ectoderm and develops into the inner portion of the body wall. The cavity between the two layers, already designated as the coelom, becomes the body cavity (peritoneal and pericardial cavities). The inner layer of the lateral plate, called the **splanchnic layer,** becomes closely applied to the endoderm. From this layer the muscular and other coats of the alimentary canal are developed. As the enteron begins to take on a tubular form within the coelom, the layers of splanchnic mesoderm of the two sides meet dorsally to it in the median line and form a dorsal **mesentery.**

From the mesoderm, especially the vertebral-plate portion, a secondary embryonic tissue, called **mesenchyme,** is given off. The mesenchyme forms the skeleton, connective tissue, smooth muscles, and the greater part of the vascular system. The skeleton of the tadpole is largely cartilage, most of which is replaced in the adult frog by bone.

The **kidney** of the young tadpole is called the **pronephros.** The pronephros appears first as a thickening (nephrotome) of the mesoderm lining the dorsal part of the body cavity on each side. This thickening becomes hollowed out to form the **pronephric** duct which at its anterior end is divided to form three pronephric tubules opening into the coelom and at its posterior end opens into the cloaca. In older tadpoles and the adult frog the pronephros disappears and is replaced by the **mesonephros.** The mesonephros first appears as a series of mesonephric tubules which communicate with the pronephric duct at one end and become enlarged at the other end. A knot of blood vessels forms and becomes pushed into the enlarged end, forming a glomerulus. During their development the mesonephric tubules acquire an opening into the coelom which, however, they later lose.

The **heart** arises in the region just behind and ventral to the pharynx from the mesoderm in a region where the splanchnic and somatic layers meet. It is at first a straight tube but later, owing to its growing more rapidly than the surrounding parts of the body, it becomes bent in the form of an S (Fig. 36:6).

The **blood vessels** develop in the mesoderm as somewhat irregular spaces which become continuous along the course which the blood vessel takes. As development advances the cells surrounding the spaces become differentiated to form the walls of the blood vessels. The arteries of the gills of the tadpole and the changes which they undergo have already been considered in the chapter on the circulation.

The **reproductive organs** first appear in the mesoderm lining the body cavity as a pair of ridges, one on either side of the dorsal mesentery. Toward the end of metamorphosis they become differentiated into ovaries or testes as the case may be.

C. METAMORPHOSIS OF THE TADPOLE INTO A FROG

The tadpole has many of the characteristics of a fish and leads a fishlike existence. After a period which varies with different species and different climate conditions, the tadpole changes into a frog (Fig. 36:9). During this change, called **metamorphosis,** the animal does not eat, and profound changes occur in its mode of life and its structure. From a water-living and mainly water-breathing animal the tadpole changes to an amphibian capable of living on land and breathing air. While the tadpole exists on a vegetable diet, the frog is carnivorous. The external morphological changes consist chiefly in the growth of fore and hind

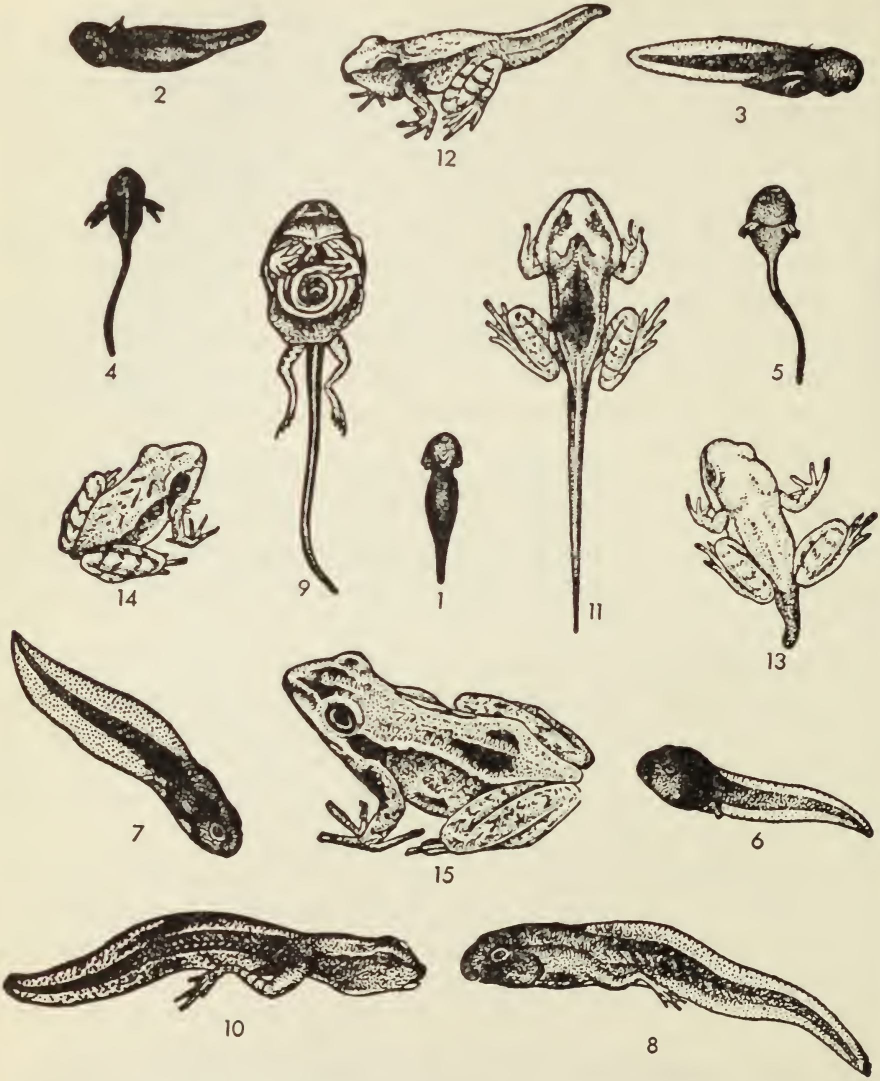

Fig. 36:9 Development and metamorphosis of a frog. 1, tadpole just hatched, dorsal view; 2, 3, older tadpoles, side views; 4, 5, later stages, dorsal views showing external gills and development of operculum; 6, older stage, showing anus; 7, older stage, showing beginning of development of hind legs; 8, 10, lateral views of two later stages, showing development of hind legs; 9, ventral view of tadpole dissected to show gills, intestine, and fore legs developed inside operculum; 11, tadpole just before metamorphosis; 12, 13, 14, metamorphosis of tadpole into frog with gradual absorption of the tail; 15, young frog just after metamorphosis. After Leuckart-Nitsche wall chart from Hegner, *College Zoology*, The Macmillan Company.

legs, the loss of the tail and changes in the size, shape, and color of the body and head. Internally even more profound changes occur. The skeleton of the tadpole consists mostly of cartilage, and during metamorphosis the change to bone occurs. The ear of the tadpole, like that of the fish, consists of an internal ear only, the sound vibrations being transmitted through the water and the tissues of the body to the endolymph. At metamorphosis the middle ear and eardrum are developed for the reception of sound waves in air. The intestine of the tadpole is long and coiled in the body cavity in a spiral resembling that of a watch spring. With the adoption of a diet consisting chiefly of the flesh of other animals a long digestive tract is no longer necessary and the intestine becomes shortened and differentiated as already described in the chapter on the digestive system.

5. THE DEVELOPMENT OF THE CHICK

A. THE EGG

The egg cell of the hen includes all of that portion which we commonly call the **yolk.** At the time of laying, if the egg has been fertilized, development has usually proceeded to a stage corresponding to that of the blastula in the frog. As is the case in the frog's egg the animal pole usually lies on top. A **vitelline membrane** surrounds the plasma mem-

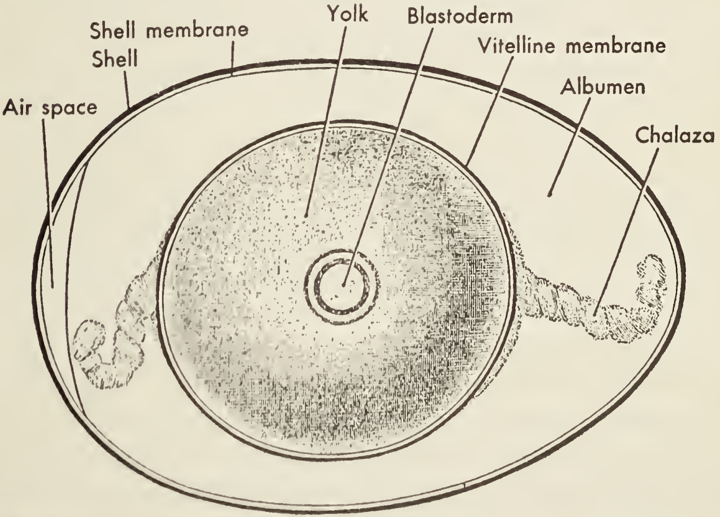

Fig. 36:10 Diagram of a longitudinal section of a hen's egg at the time of laying. The outer and inner shell membranes, which are separated by the air space, come together under the rest of the shell and are here labeled "Shell membrane." After Marshall, *Vertebrate Embryology*, by permission of G. P. Putnam's Sons.

brane and separates it from the albumen. The **albumen** or "white of egg" is outside the egg cell and is surrounded by the calcareous **shell.** Separating the albumen from the shell are two shell membranes, an **inner shell membrane** and an **outer shell membrane.** At the more rounded end of the egg the shell membranes separate and enclose an **air space** which helps in respiration during the later development. Two denser portions of the albumen in the form of coiled springlike structures called **chalazae** serve to keep the yolk in the center (Fig. 36:10). The yolk is formed in the ovary and does not increase in size after leaving the ovary of the hen. After fertilization, which occurs in the upper part of the oviduct, the yolk becomes surrounded by the albumen, shell membranes, and the shell.

B. CLEAVAGE AND EARLY DEVELOPMENT

On account of the relatively large amount of yolk in the hen's egg cleavage is restricted to a small part of the egg, called the **blastodisc,** at the animal pole which contains most of the cytoplasm, the rest of the yolk not being divided into cells. Cleavage at the animal pole leads to the formation of a disclike layer of cells called the **blastoderm,** separated from the underlying yolk by a shallow segmentation cavity or **blastocoel.** This stage corresponds to the blastula stage of the frog's egg. The presence of considerable quantities of yolk was seen to be a hindrance to gastrulation in the frog's egg. The vast amount of yolk in the hen's egg seems to make an actual invagination at the vegetal pole impossible. Endoderm is formed by an ingrowth of cells at one end of the blastoderm into the segmentation cavity. Mesoderm and a notochord are later formed in the central portion of the blastoderm between the ectoderm and the endoderm. During the early development the enteron is not enclosed but consists of a cavity overlying a portion of the yolk and bounded above by the endoderm. As development proceeds the three layers, ectoderm, mesoderm, and endoderm, gradually grow out over the yolk. The actual embryo then appears as an elongated thickening in the center of the blastoderm which consists of three germ layers, ectoderm, mesoderm, and endoderm.

A comparison of cleavage in the eggs of the starfish, frog, and chick makes it apparent that the process depends to a considerable extent on the relative amounts of yolk and cytoplasm in the egg cell. On a basis of the form which their cleavage takes, eggs have been divided into certain types. Eggs in which the cell is completely divided, as in the eggs of the starfish and frog, are said to have **total cleavage** and to be **holoblastic;**

eggs in which only a part of the contents of the vitelline membrane take part in the division, as in the case of the hen's egg, are said to have **partial cleavage** and to be **meroblastic.** When the cells formed in the process of cleavage are approximately equal, as in the egg of the starfish, the cleavage is said to be **equal.** When, as in the case of the frog's egg, smaller cells are formed at the animal pole and larger cells at the vegetal pole, the cleavage is said to be **unequal.**

C. *THE EXTRAEMBRYONIC MEMBRANES*

During their development the embryos of the starfish and frog are in water, buoyed up and kept moist by it. The eggs of birds, on the other hand, are laid on land. The hard shell makes possible the storage of large quantities of food and provides protection for the delicate embryo. Within this shell an aquatic environment is created for the embryo and means are furnished for the absorption of the food materials and the giving off of waste by the formation of membranes which are outgrowths of the germ layers of the blastoderm. Three such membranes are formed, called respectively the **amnion, allantois,** and **yolk sac** (Fig. 36:11).

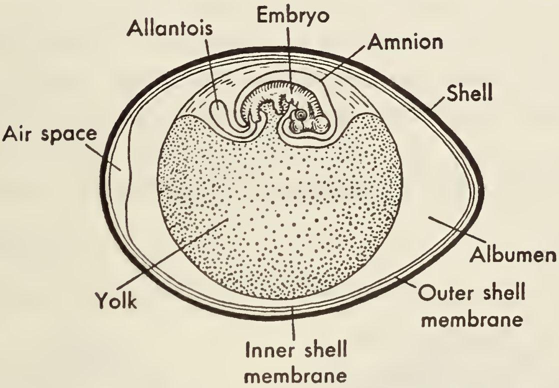

Fig. 36:11 Diagram of a longitudinal section of a hen's egg after five days' incubation, showing the development of the extra-embryonic membranes. The outer and inner shell membranes are shown as everywhere separate. In reality they are together except at the air space. The yolk is contained in the yolk sac. Redrawn after Marshall, *Vertebrate Embryology*, by permission of G. P. Putnam's Sons.

The **amnion** is developed from ectoderm and mesoderm and grows upward and over, enclosing the embryo in a cavity, the **amniotic cavity,** filled with a watery fluid, the **amniotic fluid.** It is the formation of this membrane which provides the aquatic environment referred to above in which the embryo floats and undergoes its development free to take on its characteristic form.

The **yolk sac** is formed from mesoderm and endoderm and grows downward over the yolk. This membrane becomes plentifully supplied with blood vessels and the nutriment absorbed by the endoderm from the yolk is carried in these blood vessels to the embryo. The yolk sac is continuous with the enteron of the embryo with which it connects on the under side.

Somewhat later in the development a third membrane called the **allantois** appears. It is an outpocketing of the hind gut of the embryo and like the yolk sac is formed of mesoderm and endoderm. Growing out rapidly between the yolk sac and the amnion it approaches the vitelline membrane and spreads out under it, surrounding the amnion and the greater part of the yolk sac. At the same time it becomes highly vascular by the development of numerous fine blood vessels connected with the blood system of the embryo. Its position and structure make it well adapted to carry on the function of respiration, oxygen passing through the porous shell to the blood vessels and carbon dioxide passing in the reverse direction. The allantois also functions in the absorption of albumen, and its cavity, the allantoic cavity, acts as a reservoir for the excretions of the excretory organs until the time of hatching.

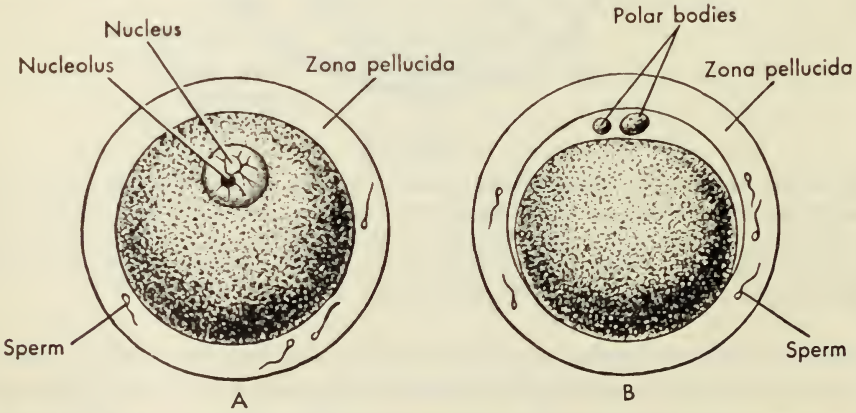

Fig. 36:12 Early development of the rabbit's egg. A, a fully formed ovum just after its discharge from the ovary; B, an ovum from the upper end of the oviduct after extrusion of the two polar bodies. After Marshall, *Vertebrate Embryology*, after Bischoff, by permission of G. P. Putnam's Sons.

6. THE DEVELOPMENT OF MAMMALS

In the chapter on reproduction reference has already been made to some of the general features of mammalian development. Having now studied the development of the frog and chick we are prepared to go into the subject in somewhat more detail.

The eggs of the most primitive living mammals, Prototheria, are relatively large (that of the duckbill, *Ornithorhynchus*, being three-quarters of an inch in their greatest diameter), are covered with shells, and are laid on the ground. These eggs contain a relatively large amount of yolk and undergo a development in which there is a partial cleavage of the egg cell and a development of extraembryonic membranes similar to what occurs in the chick. In higher (Eutherian) mammals the eggs are small (that of man is but 0.2 mm. in diameter), and contain a relatively small amount of yolk. Such eggs undergo a total and equal cleavage.

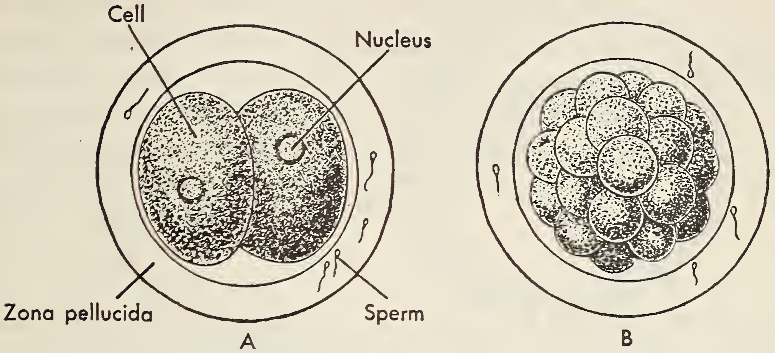

Fig. 36:13 Early development of the rabbit's egg. A, an ovum from the middle of the length of the oviduct, about twenty-two hours after copulation, showing division of the ovum into two cells; B, an ovum from the lower end of the oviduct, about the middle of the third day, consisting of a spherical mass of cells. After Marshall, *Vertebrate Embryology*, after Bischoff, by permission of G. P. Putnam's Sons.

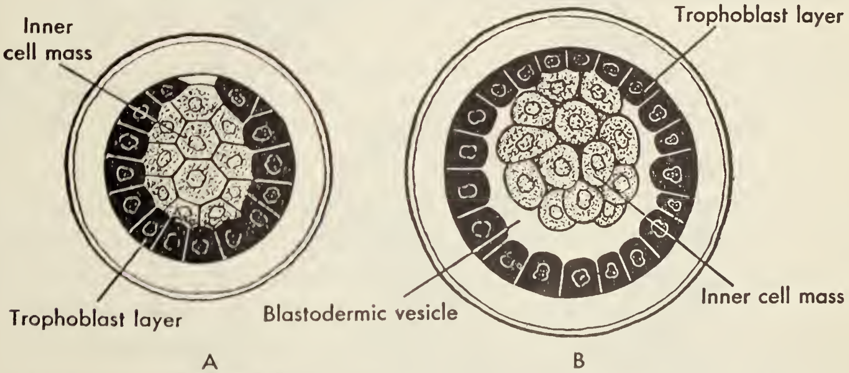

Fig. 36:14 Early development of the rabbit's egg. A, an ovum seventy hours after copulation, taken from the lower end of the oviduct just before entering the uterus. (After Van Beneden.) B, an ovum seventy-five hours after copulation taken from the uterus, and showing the first stage in the formation of the blastodermic vesicle. After Marshall, *Vertebrate Embryology*, by permission of G. P. Putnam's Sons.

The early development of the rabbit's egg may serve as an example of the process in mammals. Upon its discharge from the ovary the rabbit's egg contains a relatively large nucleus and is surrounded by a clear, noncellular membrane, called the **zona pellucida** (Fig. 36:12 A). By the time the egg has arrived in the upper part of the oviduct two polar bodies have made their appearance between the egg and the zona pellucida (Fig. 36:12 B). The polar bodies are small cells given off by the egg in its ripening process. Their significance will be discussed in more detail in Chap. 37, The Physical Basis of Heredity. The sperm enters the egg and fertilization occurs in the upper part of the oviduct. Cleavage occurs while the egg is in the oviduct, the first division dividing the egg into two practically

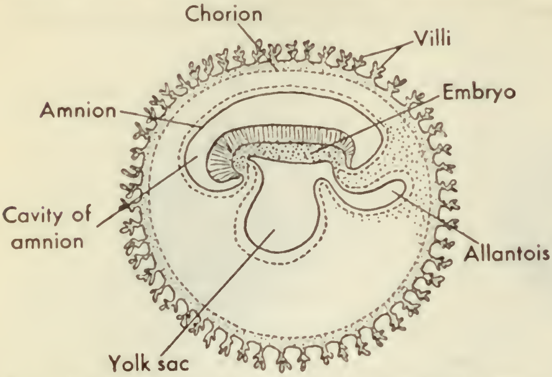

Fig. 36:15 A diagrammatic longitudinal section of a very young human embryo after implantation surrounded by the amnion and chorion, the maternal tissue of the uterus being omitted. The mesoderm of the embryonic tissues is stippled.

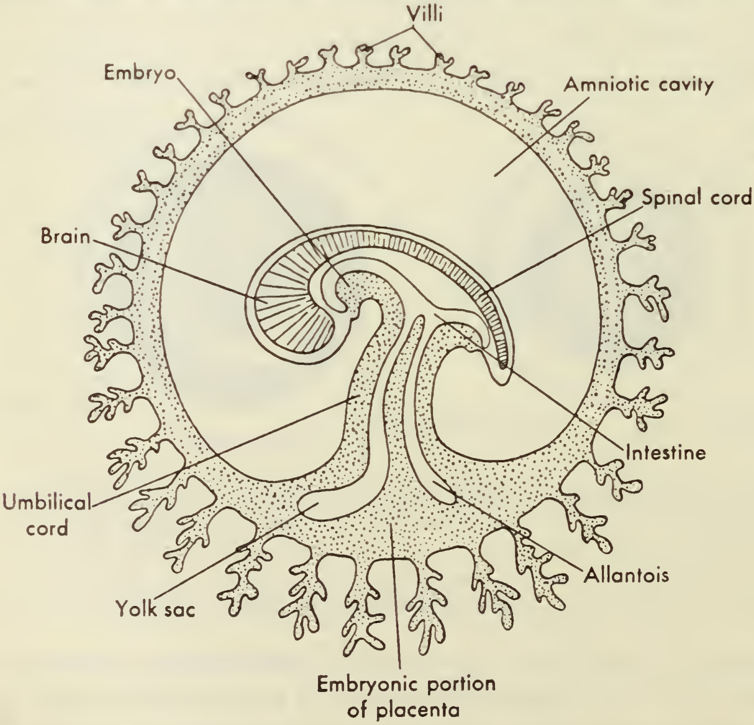

Fig. 36:16 A diagrammatic longitudinal section of a young human embryo from the uterus, showing the embryonic portion of the placenta and the umbilical cord.

equal halves (Fig. 36:13 A). Succeeding divisions lead to the formation of a spherical mass of cells, practically equal in size (Fig. 36:13 B). After further cell divisions the mass of cells becomes divided into an outer cell layer, called the **trophoblast layer** and an **inner cell mass,** the whole forming a structure called the **blastodermic vesicle** (Fig. 36:14). The formation of a trophoblast layer may be a special provision for the implantation of the egg in the wall of the uterus. From the inner cell mass, the embryo and the extraembryonic membranes, the amnion, allantois, and yolk sac, develop. The **amnion** arises at a very early stage and the embryo is soon surrounded by an amniotic cavity in which it remains during the remainder of its intrauterine life. The **yolk sac** arises also at an early stage, but as only a relatively small amount of yolk is present, remains small and soon ceases to take any active part in the nutrition of the embryo. The **allantois** early grows out toward the trophoblast layer. From the trophoblast layer, and the mesoderm which comes to underlie it, is developed a structure called the **chorion,** which becomes intimately associated with the wall of the uterus by the growth of numerous branching processes or villi (Fig. 36:15). The embryo comes to lie in the amniotic cavity connected to the chorion by the umbilical cord (Fig. 36:16).

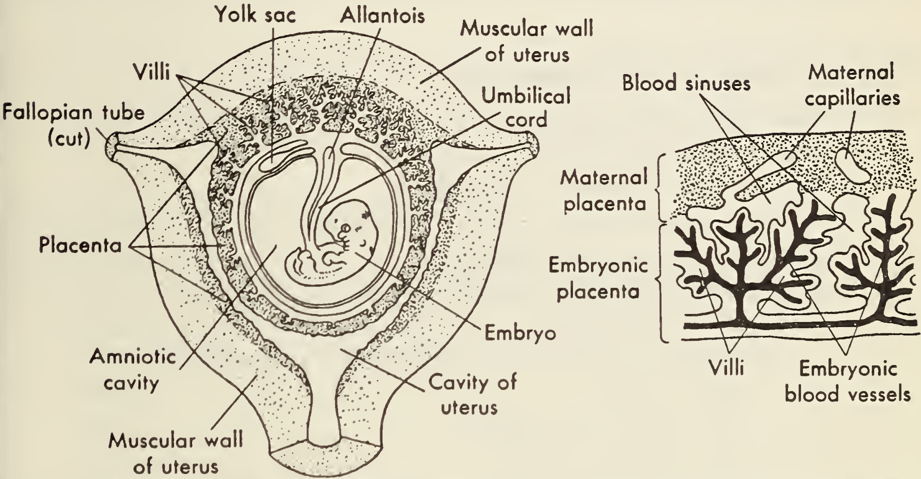

Fig. 36:17 On the left, a diagrammatic section of a human uterus in an early stage of pregnancy. On the right, a portion of the placenta, magnified to show the relation between the embryonic and maternal blood vascular systems.

The **placenta** consists of an embryonic and a maternal portion. The **embryonic portion** is formed from the chorion, the **maternal portion** from the uterine wall in the region of implantation. Blood vessels grow out from the embryo and pass through the umbilical cord to ramify in the chorionic portion of the placenta (Fig. 36:17).

It is beyond the scope of this book to describe in detail the development of mammals. It may be said, however, that there occur stages corresponding to those described in the frog, that a neural plate and a neural tube are formed, that a notochord develops, that gill pouches arise, and that the various systems of organs go through stages similar to those which the same systems pass through in the frog.

The course of development of the human embryo and foetus up to the time of birth has been briefly considered in Chap. 35, Reproduction.

Topical Outline of Chapter 36

1. The origin of the individual 673
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4. The development of the frog 677
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6. The development of mammals 692

Questions

1. Compare an egg and a sperm as regards structure and contributions to the zygote.
2. Describe the early development of the starfish.
3. Describe the early development of the frog and compare the stages with the corresponding stages of the starfish. Account for the differences.
4. List the fishlike characteristics of a tadpole.
5. Describe the development of the nervous system of the frog.

6. Describe the development of the eye of the frog.
7. Describe the development of the digestive system of the tadpole. How do the digestive systems of the frog and tadpole differ? Account for the differences.
8. Describe the development of the gill pouches and gills of the tadpole.
9. Describe the development of the mesoderm in the frog.
10. Describe the development of the pronephros or head kidney of the tadpole.
11. What changes occur at metamorphosis in the frog?
12. Compare the structure and cleavage of the egg of a chick with that of the starfish and frog and account for the differences.
13. Classify eggs according to their cleavage.
14. Describe the extraembryonic membranes of the chick and discuss the functions of each.
15. Compare the early development of the egg of a higher mammal with that of the starfish and chick. Account for the differences and resemblances.
16. Describe the extraembryonic membranes of a placental mammal and discuss the function of each. Explain the origin of the placenta.

Suggestion for Further Reading

Heuttner, Alfred F., *Fundamentals of Comparative Embryology of the Vertebrates*, The Macmillan Company, New York, 1941. A well-illustrated elementary account of vertebrate development.

CHAPTER 37

The Physical Basis of Heredity

1. LIFE CYCLES AND NUCLEAR CHANGES IN PLANTS AND ANIMALS

In studying the life cycles of plants we have already seen that in all the divisions except the Thallophytes, and in some of the latter, an alternation of generations occurs in which a sporophyte generation alternates with a gametophyte generation. These two generations differ in the methods by which they reproduce and in the chromosome content of the nuclei of their cells, the nuclei of the cells of the sporophyte being diploid, those of the gametophyte haploid. The reduction from the diploid to the haploid nuclear condition has been shown to occur during spore formation and to be associated with the complicated process of meiosis. It was also shown that the return to the diploid condition occurred as a result of the union of the gametes in fertilization and the formation of a zygote.

In animals there is, in general, no alternation of a diploid with a haploid generation such as occurs in plants. (In certain gallflies there is a curious exception which need not concern us here.) In the alternation of an asexual with a sexual generation which occurs in certain groups of the Coelenterata both generations are diploid. In animals, meiosis, including reduction from the diploid to the haploid number of chromosomes, occurs at gamete formation and the return to the diploid condition at fertilization (Fig. 37:1).

In most animals, even at an early stage in the development of the embryo, the **germ cells,** those cells which are destined to give rise to gametes, are easily distinguished from the **somatic cells,** or cells which form the various tissues and organs of the body. The germ cells never really form a functional constituent of the body of the individual. Secluded and protected in the interior of the gonads they live a life apart, unaffected by the ordinary changes which occur in the surrounding cells. Such a separation and setting apart of the germ cells does not appear to exist in plants.

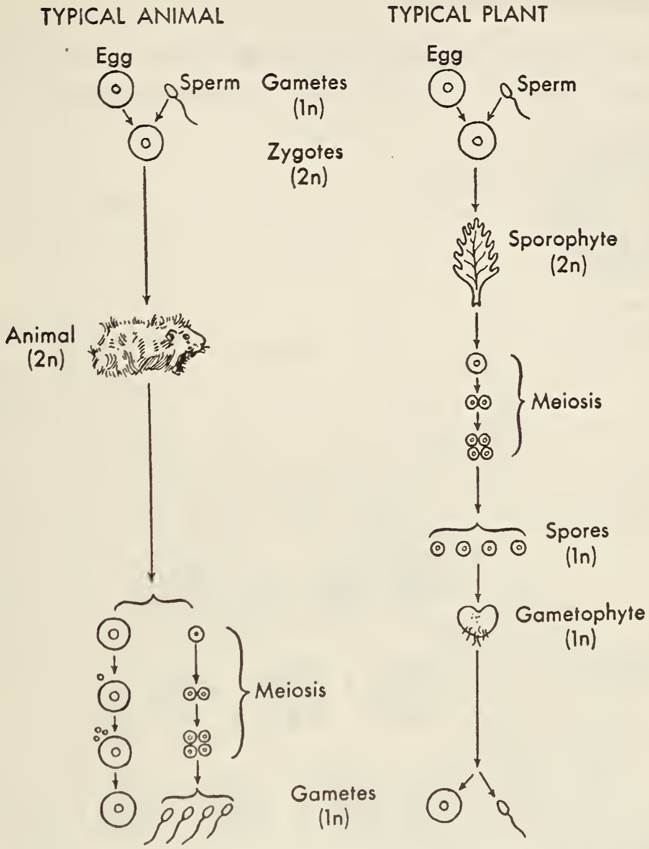


Fig. 37:1 A comparison of the nuclear changes in the life cycles of higher plants and animals. Modified after E. B. Wilson, *The Cell*, The Macmillan Company.

2. GENERAL ACCOUNT OF THE GERM-CELL CYCLE IN ANIMALS

The cells which are distinguishable in the development of the embryo as the germ cells are called **primordial germ cells.** During the development of the individual the primordial germ cells multiply by division. When the gonads develop the primordial germ cells become included in the testis or ovary and are then named **spermatogonia** or **oögonia.** After the complete differentiation of the gonads the germ cells (spermatogonia or oögonia) enter into a period of quiescence until the animal nears sexual maturity. With the approach of sexual maturity gametogenesis or gamete formation, begins. This process differs to such an extent in the two sexes that separate descriptions are necessary.

A. SPERMATOGENESIS

The entire process of spermatogenesis or the formation of spermatozoa occurs in the tubules of the testis. The spermatogonia lie in the walls of the seminiferous tubules and undergo their development into spermatozoa there (Fig. 37:2). As the animal approaches sexual maturity the spermatogonia rapidly increase in number by cell division. During the period of sexual maturity the manufacture of spermatozoa goes on con-

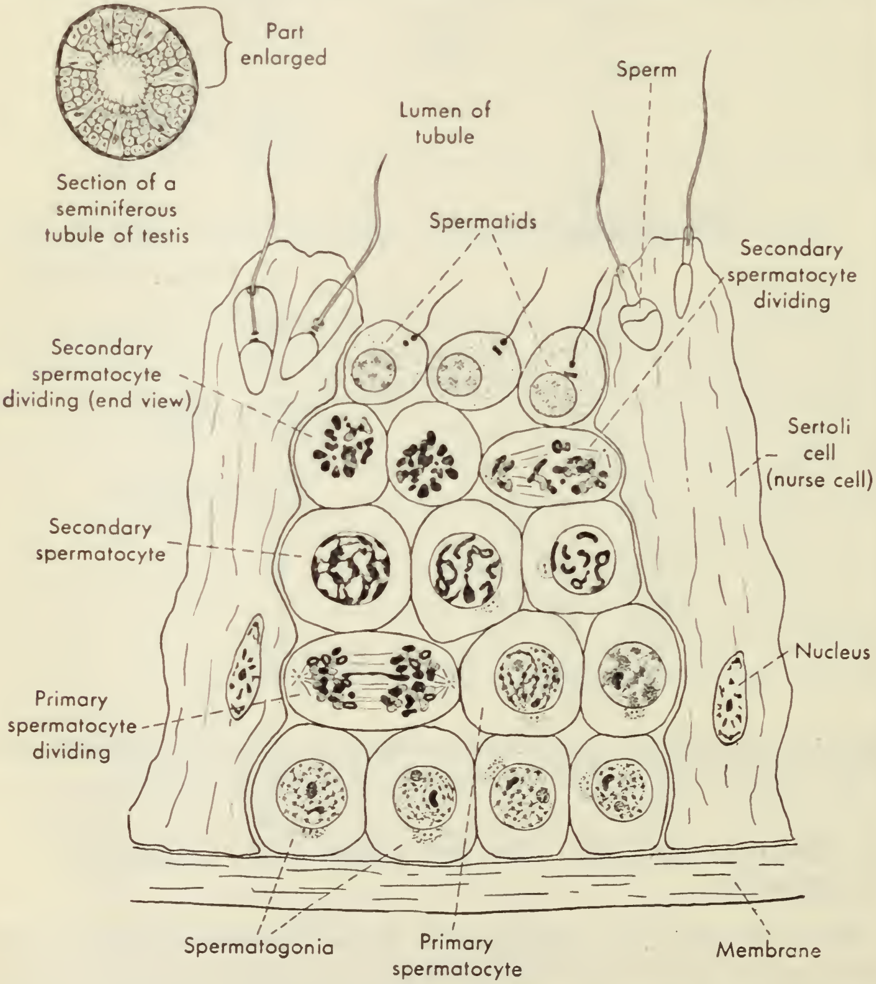

Part enlarged
Section of a seminiferous tubule of testis
Lumen of tubule
Sperm
Spermatids
Secondary spermatocyte dividing
Secondary spermatocyte dividing (end view)
Sertoli cell (nurse cell)
Secondary spermatocyte
Nucleus
Primary spermatocyte dividing
Spermatogonia
Primary spermatocyte
Membrane

Fig. 37:2 Diagram of a part of a section of a human seminiferous tubule arranged to show the different stages in spermatogenesis.

tinually. This begins when certain of the spermatogonia increase slightly in size and become **primary spermatocytes.** This change from spermatogonium to primary spermatocyte does not involve a cell division. It does, however, involve certain important nuclear changes which will be referred to later in this chapter. Each primary spermatocyte divides by a division which is called the **first maturation division** to form two **secondary spermatocytes.** Each of the two secondary spermatocytes divides by a **second maturation division** into **spermatids.** Each of the spermatids becomes differentiated into a **spermatozoon.** Thus a single primary spermatocyte gives rise by two successive cell divisions to four male gametes (Fig. 37:5).

B. OÖGENESIS

The oögonia multiply during the growth of the embryo, but in most animals there is a quiescent stage extending from birth to sexual maturity during which time there is little or no division of these cells. With the beginning of sexual maturity each oögonium becomes surrounded by one or more layers of cells which form an **ovarian follicle** (Fig. 37:3). Enclosed in an ovarian follicle the oögonium, now a **primary oöcyte,** gradually grows to be many times its original size. It is during this growth period that the yolk is deposited in the cytoplasm and that the approximate size (but not the nuclear condition) of the mature egg is reached. Thus the primary oöcytes may reach a diameter of 0.2 millimeter in a human ovary, 2 millimeters in that of a frog, and about 10 centimeters in that of an ostrich.

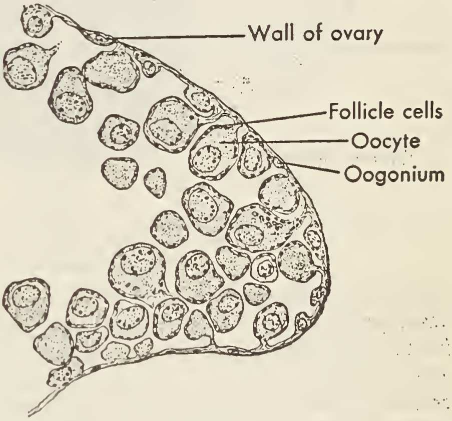


Fig. 37:3 A section through part of the ovary of a frog, *Rana pipiens.* Magnified 95 x. From Shumway, *Textbook of General Biology,* by permission of John Wiley & Sons, Inc.

The division of the primary oöcyte, the first maturation division, occurs in the frog after the egg has left the ovary and while it is in the upper part of the oviduct. This division leads to the formation of two secondary oöcytes of very unequal size. One, called the **first polar body,** is exceedingly minute in comparison to the other which retains all the yolk and is practically equal in size to the primary oöcyte. The first maturation division is followed by a division of the larger secondary oöcyte. This is called the **second maturation division.** It is also very unequal and leads to the formation of the **oötid** or **mature egg** and a minute **second polar body.** The polar bodies are usually so small in comparison to the oötid that there is practically no reduction in size of the primary oöcyte. Rarely the first polar body divides, forming two polar bodies. In this case the oötid and the three last-formed polar bodies (which may be considered to be nonfunctional oötids) correspond to the four spermatids formed in spermatogenesis. However, while in spermatogenesis all four spermatids become functional spermatozoa, in oögenesis only the oötid which receives all of the food materials stored in the primary oöcyte becomes functional. The polar bodies remain for a time attached to the mature egg but ultimately degenerate. In many animals, perhaps in most animals, one or both of the two maturation divisions occur after the oöcyte has left the ovary.

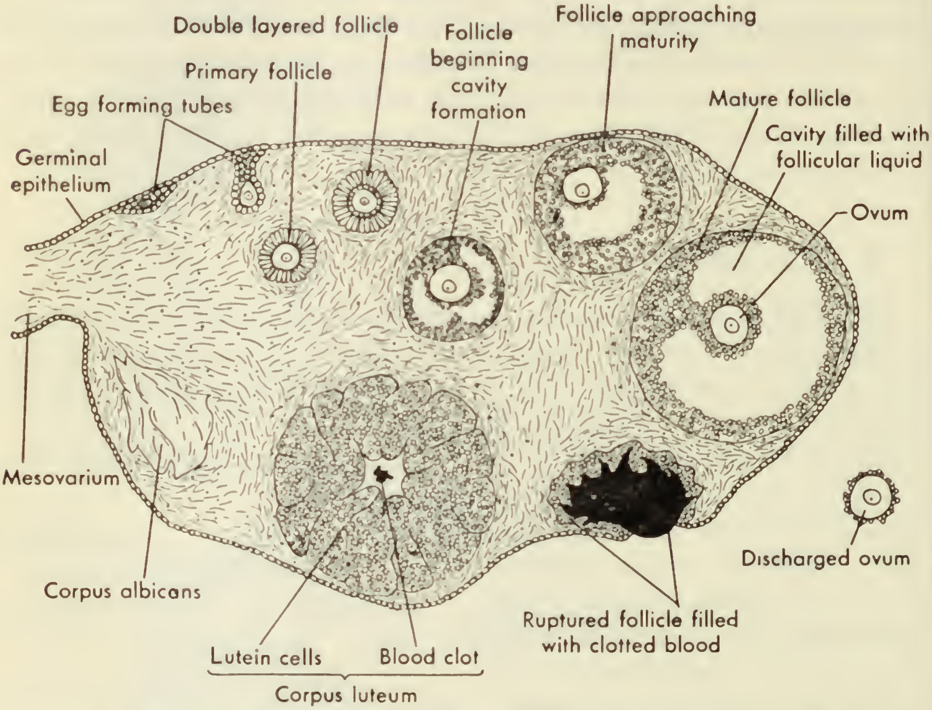


Fig. 37:4 Diagram showing the sequence of events in the mammalian ovary from the development of an ovarian follicle from the germinal epithelium to its rupture and the formation of a corpus luteum and corpus albicans. In this diagram the stages follow clockwise around the ovary, but during the actual development the follicle remains in one position in the ovary and a follicle may develop from the germinal epithelium at any point on the periphery. From Patten, *The Embryology of the Pig*, P. Blakiston's Son & Company.

On account of its particular interest in mammals oögenesis will now be described as it occurs in that group (Fig. 37:4). Surrounding the ovary and acting as its outer epithelial layer is the **germinal epithelium.** Within this are the connective tissue cells which form the **stroma** or ground tissue of the ovary. Oögonia appear in the germinal epithelium and are gradually forced down into the ovary by cells from the germinal epithelium which form **ovigerous tubes** extending into the stroma. The oögonia, surrounded by cells from the germinal epithelium, become separated from the latter as **egg nests.** The egg nests break up and the oögonia become separated, each surrounded by its layer of germinal cells which now form a follicle consisting of a sphere of follicle cells in the center of which is the oögonium. As the follicle is formed the oögonium begins to grow in size and to develop into a primary oöcyte. The follicle cells divide and give rise first to a two-layered and then to a multiple-layered follicle. Between the layers of the follicle cells spaces

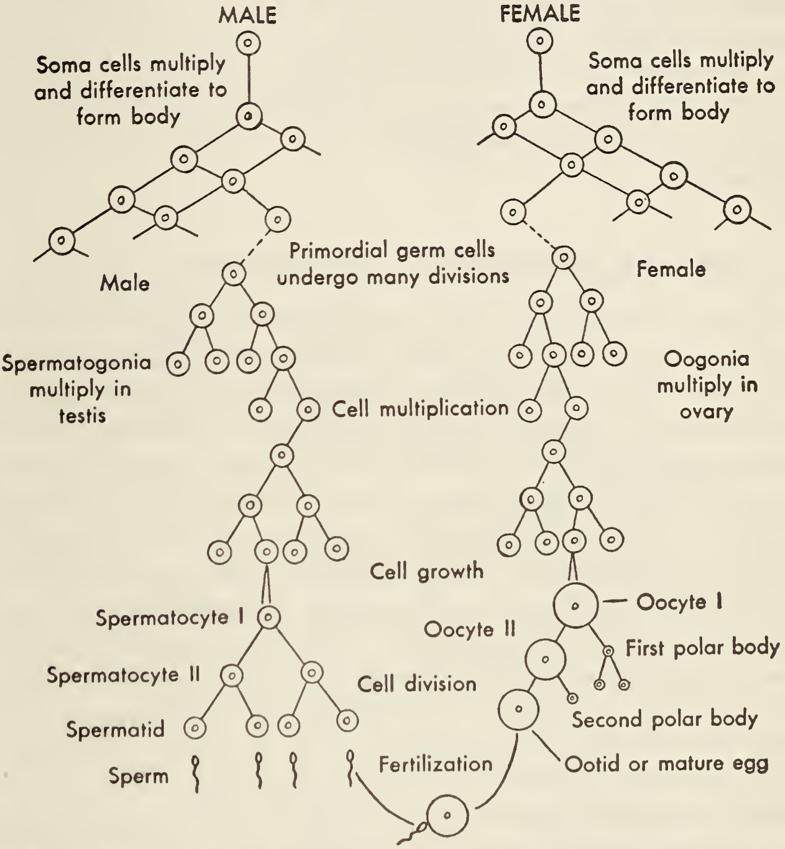

MALE
FEMALE
Soma cells multiply and differentiate to form body
Soma cells multiply and differentiate to form body
Male
Primordial germ cells undergo many divisions
Female
Spermatogonia multiply in testis
Oogonia multiply in ovary
Cell multiplication
Cell growth
Spermatocyte I
Oocyte I
Oocyte II
First polar body
Spermatocyte II
Cell division
Spermatid
Second polar body
Sperm
Fertilization
Ootid or mature egg

Fig. 37:5 Diagram illustrating the germ-cell cycle in an animal.

appear which fuse to form a continuous cavity into which the oöcyte projects, surrounded by follicle cells. Such a follicle is called a **Graafian follicle.** The development of the Graafian follicle and the process of ovulation are controlled by the **gonadotropic hormone,** secreted by the anterior lobe of the hypophysis. When the development of the Graafian follicle is completed its outer wall ruptures and the oöcyte surrounded by follicle cells is liberated into the coelom. After the liberation of the oöcyte the Graafian follicle becomes filled with a blood clot. The blood clot is then gradually absorbed and the cells of the follicle develop into the **corpus luteum,** already referred to in the chapter on reproduction.

C. NUCLEAR CHANGES IN THE GERM-CELL CYCLE

In all animals, except in a few special cases, the nuclei of the somatic cells and of the germ cells up to and including the primary spermatocytes and primary oöcytes are diploid, i.e., they contain homologous pairs of chromosomes, one member of the pair being of paternal the other of maternal origin. Also the division of these nuclei up to this point is by the process of mitosis described in Chap. 4. Similarly in all bryophytes, pteridophytes, and spermatophytes the nuclei of all of the cells of the sporophyte generation up to and including those of the spore mother cells are diploid and nuclear division up to this point is by ordinary mitosis. The two succeeding divisions of the nucleus which lead to the formation of gametes in animals and spores in the plants follow a pattern which differs from ordinary mitosis and in consequence is termed **meiosis.** Meiosis is fundamentally the same in plants and animals, although there are variations in the details (Fig. 37:6).

Animal spermatogenesis may be considered first. In the prophase of the primary spermatocyte, i.e., at the beginning of the first maturation division, each of the chromosomes appears to be split longitudinally into two chromatids as in ordinary mitosis. However, at about the same time, or a little later, in the prophase, homologous chromosomes come together in pairs with their long axes approximately parallel and the chromosomes more or less coiled about each other. This association of homologous chromosomes is called **synapsis.** Due to the splitting of the chromosomes and synapsis the pairs of homologous chromosomes in the nucleus of the primary spermatocyte are replaced by groups of chromatids, four chromatids in each group. Such a group of four chromatids is called a **tetrad.** The splitting of the chromosomes at the beginning of the maturation division is the only division of the chromosomes in the whole process of meiosis, the subsequent nuclear divisions serving only to distribute each of the four chromatids of a tetrad, one to each of the four spermatids. In the anaphase of the first maturation division each of the tetrads is divided. Thus in the nuclei of the secondary spermatocytes the chromatids occur in groups of two, called **dyads.** In the division of the secondary spermatocytes to form spermatids the chromatids of the dyads separate and become the chromosomes of the spermatids and eventually the chromosomes of the sperm cells. Apparently any chromatid may go to any spermatid, so that in a sperm any one of the chromosomes may be of either maternal or paternal origin.

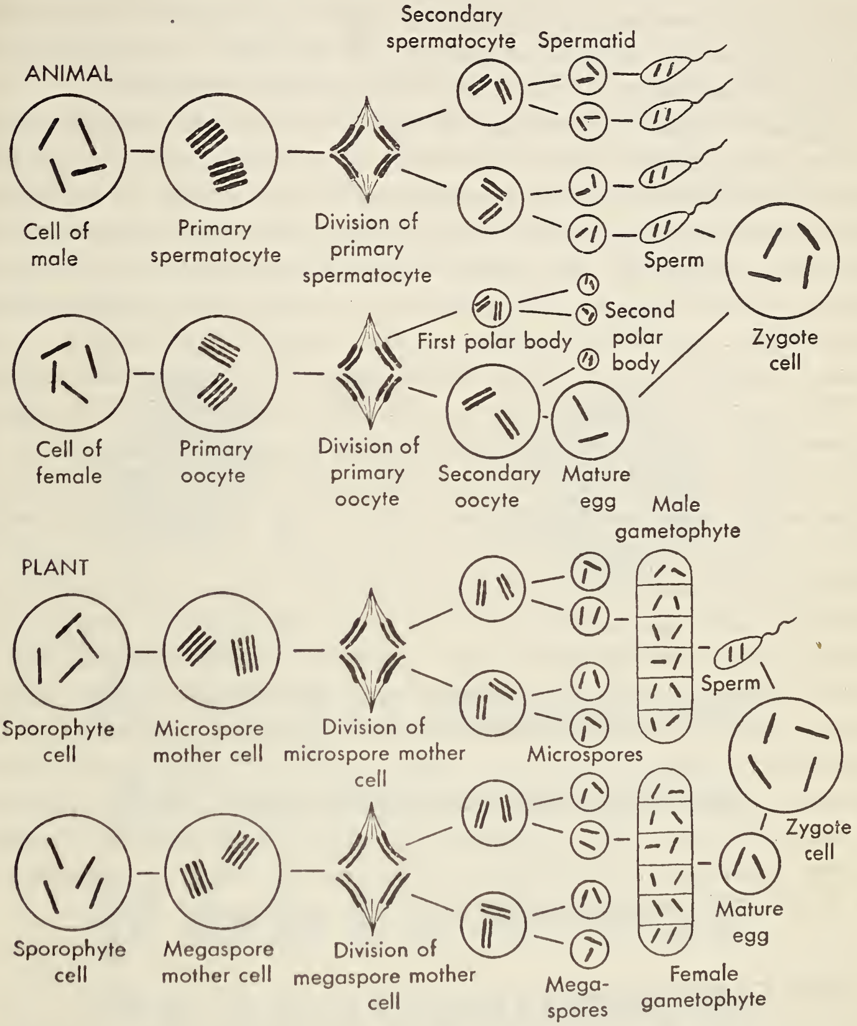


Fig. 37:6 Comparison of the germ-cell cycles in animals and plants. The somatic number of chromosomes has been assumed to be four in each case.

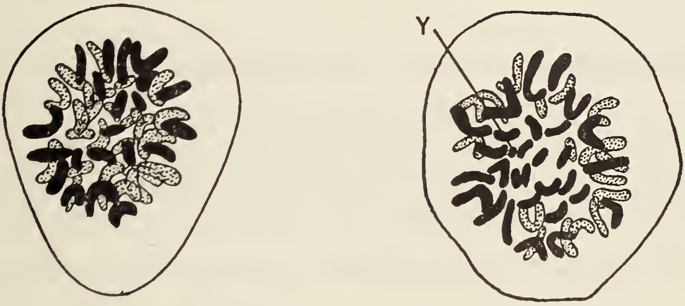
Meiosis as it occurs in **animal oögenesis** is practically identical with spermatogenesis just described. Synapsis occurs and tetrads are formed in the primary oöcyte. In the first maturation division the tetrads form dyads and in the second maturation division the dyads divide to form single chromosomes so that the oötid or mature egg and the second polar body contain the haploid number of chromosomes. A comparison of mitosis and meiosis may help in following the above discussion.

In **plants** meiosis is essentially the same as in animals. Synapsis occurs in the spore mother cells, and tetrads are formed there. In the first maturation division the tetrads are divided to form dyads. In the second maturation division the dyads divide to give the single chromosomes of the spores, which like the eggs and sperms of animals are haploid. It should be noted that in some plants there is no visible splitting of the chromosomes until after synapsis so that tetrads do not appear to be formed although the process of meiosis appears to be otherwise similar.

The results of meiosis may be summarized as follows: (1) The diploid chromosome number of the spermatogonia and oögonia is reduced to the haploid number found in the mature germ cells. (2) The chromosomes which occur in homologous pairs in the diploid nucleus occur only as single chromosomes in the mature germ cells so that except in certain special cases a germ cell never contains two homologous chromosomes. (3) The chromatids from a tetrad are distributed at random one to each of the resulting sperm, eggs, or spores, as the case may be. Since in any individual animal, one member of a pair of homologous chromosomes can be traced to the father and the other to the mother of the individual, it follows that in any mature germ cell produced by an individual any one of the single chromosomes may be of either paternal or maternal origin. This, as will appear later, has an important bearing on the transmission of hereditary characteristics which are believed to be determined by certain bodies in the chromosomes.

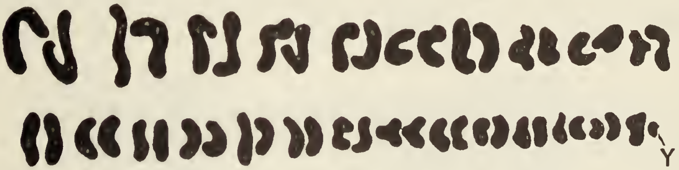
3. THE CHROMOSOMES

In the description of mitosis in Chap. 4 and again in the account of meiosis in this chapter, the chromosomes are seen to play a leading role. We now propose to study these important structures in more detail and will begin with a brief review of their history. In most cells it is not possible to recognize the chromosomes in the resting stage of the nucleus. The chromosomes first become recognizable in the beginning of the prophase of a cell division when they appear as condensations of the scattered chromatin granules of the resting nucleus into fine, tangled, threadlike bodies. Each of these threadlike chromosomes splits longitudinally and at the end of the prophase is represented by two deeply staining, rodlike structures adhering to each other longitudinally. In this condition they become arranged on the equatorial plate in the metaphase. The two rodlike structures separate during the anaphase and go to opposite poles of the division figure. During the telophase the chromosomes gradually swell up and become irregular, rounded vesicles in which the chromatin granules are scattered. At the end of this phase the vesicles at each pole coalesce to form a new nucleus in which the chromatin granules are scattered in an irregular network, and the boundaries of the chromosome vesicles are no longer visible. This is what usually happens. However, in a few cases persistent chromosome vesicles have been observed in the resting stage of the nucleus.

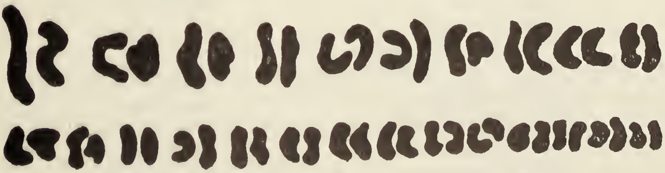


A, a diploid cell from a woman

B, a diploid cell from a man



C, Chromosomes in a diploid cell from a man



D, Chromosomes in a diploid cell from a woman

Fig. 37:7 Chromosomes of the human male and female. A, a cell from a woman showing forty-eight chromosomes, two of which are presumably X-chromosomes; B, a cell from a man showing forty-eight chromosomes, one of which is the Y-chromosome and another presumably an X-chromosome; C, the forty-eight chromosomes from a cell of a man, separated and arranged to show their occurrence in pairs. Note the Y-chromosome at the end of the series. D, the forty-eight chromosomes from a cell of a woman, separated and arranged to show their occurrence in pairs, the pair of chromosomes at the end of the series are thought to be X-chromosomes. All figures after Evans and Swezy, *The Chromosomes in Man, Sex and Somatic*, by permission of the University of California Press.

A. CHROMOSOME NUMBER

Reference has already been made to the fact that each species of animal or plant has a certain constancy in the number and characteristics of its chromosomes. Table 37:1 gives the chromosome numbers of some common animals and plants chosen from different groups. It will be noticed that there is no correspondence between the numbers of chromosomes and the amount of differentiation or evolutionary development shown in the group. In man in the somatic cells and in the spermatogonia and oögonia the chromosomes number forty-eight or twenty-four pairs (Fig. 37:7).

B. THE GENETIC CONTINUITY OF THE CHROMOSOMES

From the above description it will be seen that in most cases we lose sight of the chromosomes during the resting stage of the nucleus. This is the stage in which the nucleus passes most of its existence and during which the morphological differentiation of the cytoplasm of the cell occurs. We are therefore faced with the problem of what becomes of the chromosomes in the resting stage of the nucleus and whether the chromo-

TABLE 37:1. NORMAL CHROMOSOME NUMBERS FOR A NUMBER OF SPECIES [1]

COMMON NAME	SPECIES	GROUP	DIPLOID NUMBER
Animals			
Sponge	*Sycandra sp.*	Porifera (sponges)	16
Hydra	*Hydra fusca*	Coelenterata	12
Roundworm	*Ascaris megalocephala univalens*	Nemathelminthes	2
Planarian	*Dendrocoelum lacteum*	Platyhelminthes	14
Earthworm	*Lumbricus herculeus*	Annelida	32
Clam	*Unio sp.*	Mollusca	32
Crayfish	*Cambarus virilis*	Crustacea	200
Fruit fly	*Drosophila melanogaster*	Insecta	8
Dogfish	*Scyllium canicula*	Pisces	24
Bullfrog	*Rana catesbiana*	Amphibia	26
Hen	*Gallus domesticus*	Aves	18
Dog	*Canis familiaris*	Mammalia	52
Man	*Homo sapiens*	Mammalia	~~48~~ 46
Plants			
Alga	*Spirogyra neglecta*	Algae	24
Liverwort	*Riccia lutescens*	Bryophyta	8
Moss	*Bryum capillare*	Bryophyta	20
Fern	*Pteris aquilina*	Pteridophyta	64
Lily	*Lilium martagon*	Spermatophyta	24
Corn	*Zea mays*	Spermatophyta	20

[1] Selected from a more extensive table in E. B. Wilson, *The Cell in Development and Heredity*, The Macmillan Company, New York, 1925.

somes are genetically continuous, i.e., whether they continue to exist as individual chromosomes throughout the life of the cell.

Two lines of evidence indicate the genetic continuity of the chromosomes. The first is their regular recurrence at each division of the nucleus with identical morphological characteristics. The second line of evidence is the location in the chromosomes of the genes or determiners of hereditary characters. As will be shown in Chap. 38, Heredity, not only have the genes (cell constituents which correspond to hereditary characteristics) been shown to reside in the chromosomes, but in certain cases their positions in the chromosomes have been determined. These determinations have shown that the genes maintain the same position in the chromosomes from cell division to cell division and generation to generation except in certain special cases to be considered later.

C. THE FINER STRUCTURE OF THE CHROMOSOMES

On account of their great importance much interest is attached to the finer structure of the chromosomes and attempts to identify the genes in them. It cannot be said that any gene has yet been identified with certainty, but recent investigations have determined within narrow limits the position in the chromosome of certain genes and it seems likely that their identification is not far off.

The finer structure of the chromosomes is best seen in the prophase stage in which they extend as long fine threads. In these threads the chromatin material takes the form of small irregular masses which in some cases appear as large granules and in others as bands. In the salivary glands of flies (Diptera) are large cells with large nuclei. These nuclei contain gigantic chromosomes. The chromosomes of the salivary glands of the fruit fly *Drosophila* have recently been studied in great detail. Since the fruit fly is also a very favorable object for the study of heredity it is possible to correlate the cytological findings regarding the

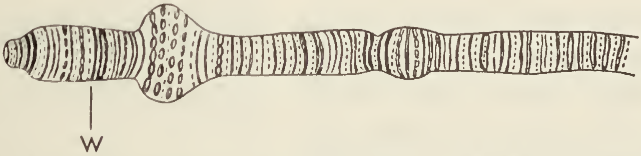


Fig. 37:8 Part of an X-chromosome of the salivary gland of the fruit fly, *Drosophilia mealanogaster*, very highly magnified showing the banded structure and the approximate location of the gene for white eye color (W) as determined by combined results of breeding experiments and microscopical investigations. Redrawn from an article in the *Journal of Heredity* by C. B. Bridges, by permission.

structure and structural changes with the behavior of the genes in heredity.

In the illustration (Fig. 37:8) the chromatin is arranged in dark bands which cross the chromosome. (Whether these "bands" are discs extending through the chromosome or rings surrounding it is not certain.) A considerable number of genes have been located along the length of this chromosome. At or very near the band marked "W" is located a gene which is responsible for certain eye colors. In what is regarded as the normal condition of this gene the eyes are red, in another and different condition of the gene the eyes are white, in yet another condition of the gene they are a yellowish red (eosin). Precisely how the gene in the chromosome acts to produce the color in the eye is not known, but that it does so is clearly established by experimental breeding and cytology.

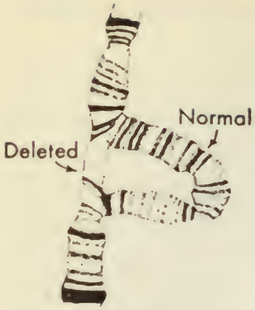


Fig. 37:9 Parts of two chromosomes in synapsis to show how corresponding regions of the chromosomes come together. This is made more conspicuous by the fact that a part of one of the chromosomes is "deleted," i.e., missing. From the salivary gland of the fruit fly *Drosophila melanogaster*. From an article by Painter in the *Journal of Heredity*, by permission.

4. SYNAPSIS

One of the most significant features of meiosis is **synapsis.** As already stated this consists of a pairing of homologous chromosomes and occurs in the primary spermatocytes and oöcytes during the growth periods. In those cases where synapsis can be most clearly observed the union between the chromosomes seems to be a very intimate one and to be such that corresponding parts of the chromosomes are united. When, as sometimes occurs, a short region is missing from one of the chromosomes of a pair united in synapsis, the union occurs so that only identical parts of the chromosomes unite and the part of the chromosome without a corresponding part in the other chromosome hangs out as a free loop (Fig. 37:9).

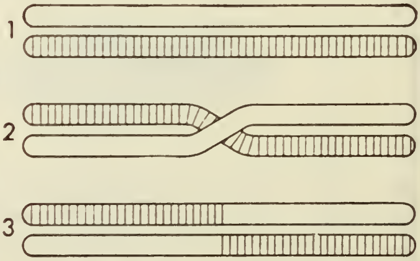


Fig. 37:10 Diagram illustrating the explanation of crossing over as due to the twisting of chromosomes. The chromosomes are supposed to become attached at some point, then to break and the pieces of different chromosomes to recombine as indicated. The white chromosome may be regarded as having come from one parent, the crosshatched as having come from another. After Shull, *Heredity*, McGraw-Hill Book Company, Inc.

Synapsis is of great importance in the transmission of hereditary characters. It is now known that during this process, or as a result of it, portions of the chromosomes with their contained genes may be interchanged, so that a part of one of the chromosomes with the genes which it contains may change places with the corresponding part of the chromosome with which it is synapsed. This phenomenon, called **crossing over,** can be demonstrated in breeding experiments and will be referred to in the next chapter (Fig. 37:10).

5. FERTILIZATION

A. THE UNION OF SPERM AND EGG

In a previous chapter experiments were cited which indicated that in bryophytes and pteridophytes the sperm was attracted toward the egg in the archegonium by some chemical substance, possibly malic acid. There is evidence that the growth of the pollen tube in flowering plants is also a chemotropic phenomenon. In animals the matter seems to be otherwise. Experiments directed to determine what, if any, chemical substances were involved have given negative results and it is now generally believed that in the case of animals the sperm reaches the egg by accident, but having once touched it remains in contact until it penetrates the vitelline membrane. In most eggs the entrance of a single sperm produces an immediate change in the egg so that other sperm do not enter. This seems to be partly but not entirely due to the formation by the egg of a fertilization membrane through which the sperm are unable to pass. Usually the entire sperm enters the egg but in some cases, for example the sea urchin and the starfish, a part of the tail is left outside (Fig. 37:11).

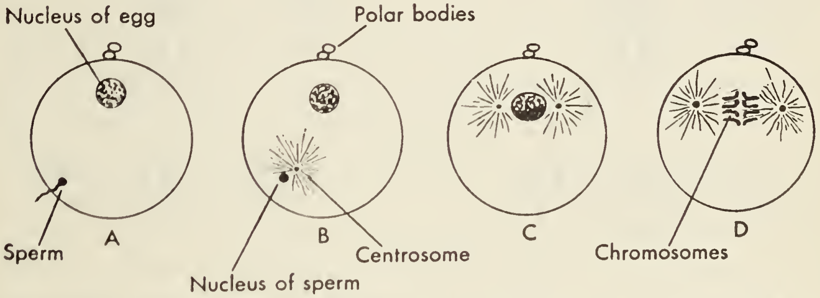


Fig. 37:11 Diagram illustrating fertilization. A, sperm entering mature egg; B, sperm nucleus and centrosome (from middle piece of sperm) approaching egg nucleus; C, sperm nucleus fusing with egg nucleus, centrosome divided; D, first nuclear division in zygote.

B. THE CONTRIBUTIONS OF THE GAMETES

Although the contributions of the egg and sperm toward the chromosomes of the nucleus of the zygote are in most cases approximately equal while not exactly the same, the cytoplasmic contributions are markedly different. In the egg the cytoplasm seems to be mainly concerned with the storage of food materials for the future embryo. In the sperm the cytoplasm is small in amount and represented only by the tail and middle piece, this gamete being adapted for locomotion. The centrosome of the zygote is contributed by the sperm of which it constitutes the middle piece. The mature egg is without a centrosome.

6. SEX DETERMINATION

In many animals and some plants the nuclei of the cells of the female have been found to differ in their chromosome constitution from those

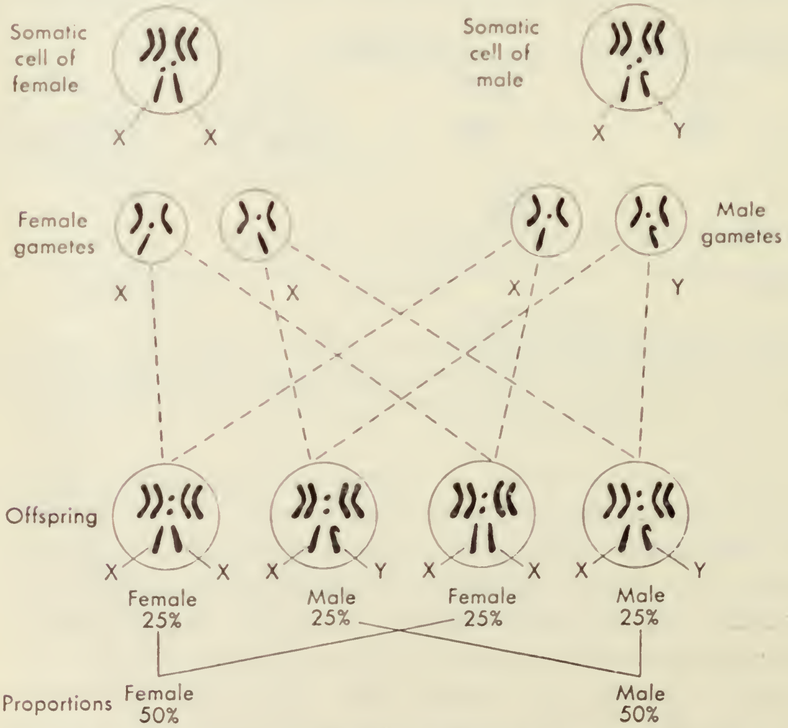


Fig. 37:12 Sex determination as illustrated in the fruit fly, *Drosophila melanogaster*.

of the male. We may take as an example the fruit fly, *Drosophila*. The difference between the male and the female set of chromosomes is found in one of the pairs of chromosomes, called on this account the **sex chro-**

mosomes, the other chromosomes being called **autosomes.** In the female the sex chromosomes, which are designated the X-chromosomes, are exactly alike while in the male one sex chromosome designated also the X-chromosome is exactly like the two X-chromosomes of the female while the other member of the pair designated the Y-chromosome is different in shape (Fig. 37:12). It has been proved that the "femaleness" of a female individual is in large part due to the presence of the two X-chromosomes, while "maleness" of a male individual is in large part due to its possessing only one X-chromosome.

The method by which sex is determined in the fruit fly can be best understood by following the sex chromosomes through the germ-cell cycle (Fig. 37:12). Since the cells of the female each contain two X-chromosomes, the mature eggs must each contain one X-chromosome and in this respect are all alike. The cells of the male each contain one X-chromosome and one Y-chromosome. When spermatozoa are formed they are of two types, one type containing one X-chromosome and the other type containing a Y-chromosome. It is clear also that the two types occur in equal numbers. When, therefore, an egg is fertilized, there is an equal chance of either a sperm containing an X-chromosome or a sperm containing a Y-chromosome uniting with it. If it is fertilized by a sperm containing an X-chromosome, the cells of the resulting zygote will contain two X-chromosomes and the individual will be a female. If, on the other hand, it is fertilized by a sperm containing a Y-chromosome, the cells of the zygote will contain an X-chromosome and a Y-chromosome and the individual will be a male. It has been proved by microscopic examination of the germ cells that the method above outlined is the method, with certain differences of detail, by which sex is determined in many animals, including man. It is thus seen that sex, in most cases at least, is determined at the time of fertilization and that it is determined by the chromosomes.

7. PARTHENOGENESIS

In certain cases eggs may cleave and develop into mature individuals without having united with a sperm. This is called **parthenogenesis** (Gr. *parthenos*, a virgin + *genesis*, to be born) and occurs regularly in certain animals. Reference has already been made to the fact that the male bee or drone always arises from a mature but unfertilized egg. Its cells are haploid and when spermatozoa are formed in its testes there is no meiosis and no reduction of the chromosomes. Numerous other examples of **natural parthenogenesis** could be cited. In some cases the egg may develop without completing the maturation process and the resulting individual be diploid.

Various methods, both chemical and physical, applied to sea urchins and other eggs have been found to produce **artificial parthenogenesis.** As in the case of natural parthenogenesis, development may be initiated either before or after maturation and lead to either diploid or haploid individuals respectively.

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Questions

1. Compare the life cycle of a typical higher plant with that of a typical higher animal.
2. Make a diagram comparing the general cellular features of spermatogenesis and oögenesis, and state in what part of the body of the animal each stage occurs.
3. Compare the nuclear changes in the germ-cell cycle of a typical animal and a typical higher plant.
4. Describe a chromosome and discuss the changes which the chromosomes undergo in the life cycle of an animal.
5. Does the number of chromosomes bear any relation to the evolutionary status of an animal or plant? Illustrate your answer by examples.
6. What evidence is there that the chromosomes exist individually from one cell division to the next?
7. Where are the genes?
8. Describe meiosis in an animal.
9. Explain the chromosomal mechanism of sex determination.
10. Define parthenogenesis. Give examples of natural and artificial parthenogenesis.

CHAPTER 38

Heredity

1. REPRODUCTION AND HEREDITY

We have already seen numerous examples of how plants and animals may reproduce by sexual and asexual reproduction. In all cases of **asexual reproduction** the new individual arises from a portion of the parent individual without any fusion of gametes. Such an individual, in so far as the constitution of its protoplasm and the nuclei of its cells is concerned, is the same as the parent from which it arose. On the other hand, in the case of **sexual reproduction** the new individual arises from the fusion of two gametes, and the resulting zygote contains living material from each of the two parents. The study of heredity is concerned chiefly with the likenesses and differences which result from the sexual method of reproduction.

Our study of sexual reproduction has shown us that the only way in which a characteristic can be transmitted from parent to offspring is through the gametes. The characteristic, as such, is not actually passed from parent to offspring. What is transmitted is the tendency for the particular characteristic to develop in the offspring. The material basis of this tendency has been called the **gene.** Thus the hereditary factors or genes pass from one generation to another in the gametes. In the previous chapter the genes were stated to be located in the chromosomes.

2. HEREDITY AND VARIATION

It is common experience that in the organic world like begets like, that from a hen's egg can come only a chicken, that the seeds of a wheat plant will produce only wheat plants. Reproduction is one of the characteristics of living organisms which distinguishes them from inanimate things and reproduction implies heredity. Nevertheless, animals and plants of the same species or the same race are not exactly alike; each one differs, if only slightly, from the other. Thus while heredity ensures that the individuals of the species shall in general be alike and that the characteristics of the species shall be maintained, there is, nevertheless, a tendency for individuals to differ from each other. This tendency is called **variation.**

3. KINDS OF VARIATION

Two kinds of characters may be grouped under the general name of variations: (1) characters which are due to **differences in the environment** under which the individuals have developed, (2) characters called **mutations** which have arisen suddenly in a single individual without particular relation to the environmental conditions. The differences between these two kinds of variations can be most clearly understood by considering examples.

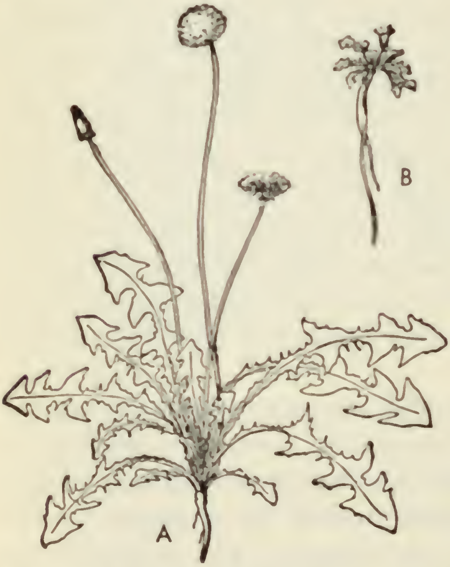


Fig. 38:1 Variation produced by the environment. A, plant of the dandelion (*Taraxacum*) grown in a lowland garden; B, portion of the same plant grown in an alpine garden under relatively unfavorable conditions. After Bonnier, from Sinnott and Dunn, *Principles of Genetics*, by permission of the McGraw-Hill Book Company.

A. CHARACTERS DUE TO DIFFERENCES IN THE ENVIRONMENT

Many plants can be grown by "cuttings." A portion cut from a plant is planted and gives rise to a new plant. Figure 38:1 shows two plants, one grown from a cutting from the other. The original plant, A, in the figure, was grown in a lowland garden under relatively favorable conditions. The plant raised from the cutting was grown in an alpine garden under relatively unfavorable conditions. The two plants differ in a number of characters, including size, length of the flower stalks, and the shape of the leaves. A cutting from B grown under favorable lowland conditions would, there is every reason to believe, produce a plant like A. Characters which like these are due to differences in the environment are often called **acquired characters.**

The following experiment shows the effect of the environment in inducing an acquired character in an animal. When eggs of the small fish *Fundulus* are raised in sea water containing various salts of magnesium, curious but characteristic modifications occur. The eyes tend to be defective and to move toward the median line. In extreme cases the eyes may become fused, producing a condition similar to that attributed to the giant *Cyclops*. The condition is not inherited and it is difficult to see how the modification could possibly be interpreted as an adaptation to the environment. Many similar cases could be cited.

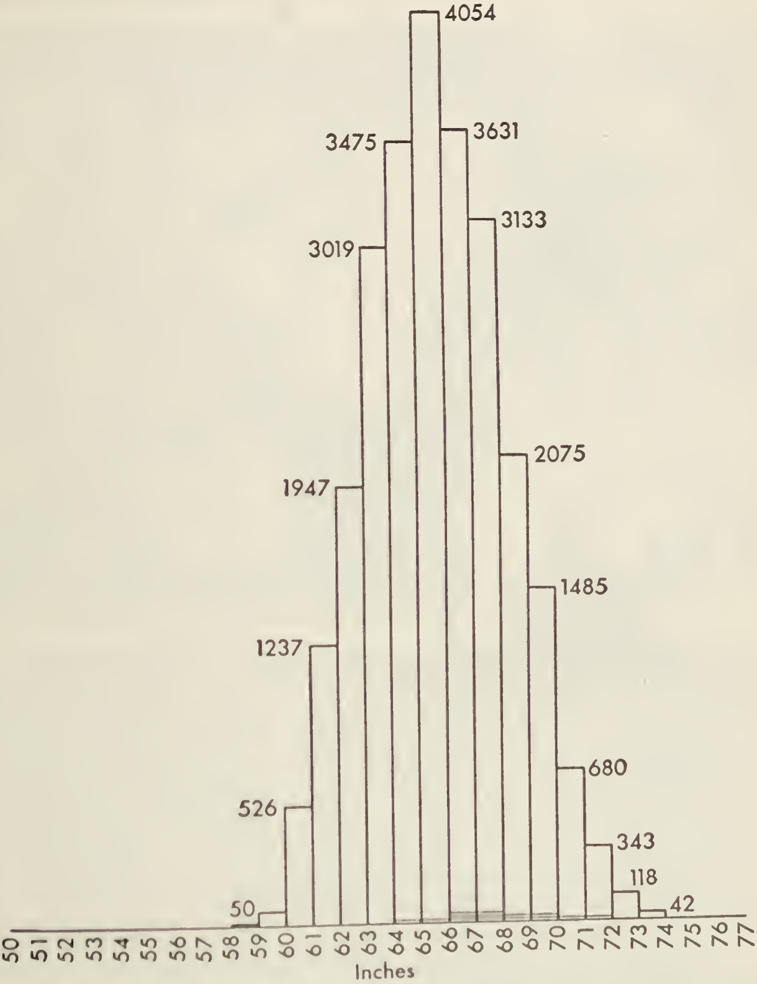


Fig. 38:2 Variation in heights of United States army recruits. The horizontal scale represents the height in inches. The vertical columns represent the total number of individuals of each height. After C. B. Davenport from Popenoe and Johnson, *Applied Eugenics*, The Macmillan Company.

The two examples cited, viz., the dandelion grown in an alpine climate and the *Fundulus* eggs treated with magnesium salts, are extreme cases. Less conspicuous cases occur everywhere. Indeed, as already stated, no two organisms of the same species are exactly alike. However, all normal individuals of a given species tend to conform to a certain type and in many cases variation about this type lends itself to exact study. Men vary in height. The height in inches of a group of United States Army recruits is shown graphically in Figure 38:2. Although the heights varied from 58 inches (4 feet, 10 inches) to 74 inches (6 feet, 2 inches), individuals of these extremes are very rare. The most frequent height, called the **mode,** is between 65 and 66 inches, or between 5 feet, 5 inches, and 5 feet, 6 inches. The mode is not the same as the **average.** The average height is determined by taking the sum of all the individual heights and dividing by the number of men. In the example chosen, the average height comes within the limits of the mode. This variation is not entirely due to environment.

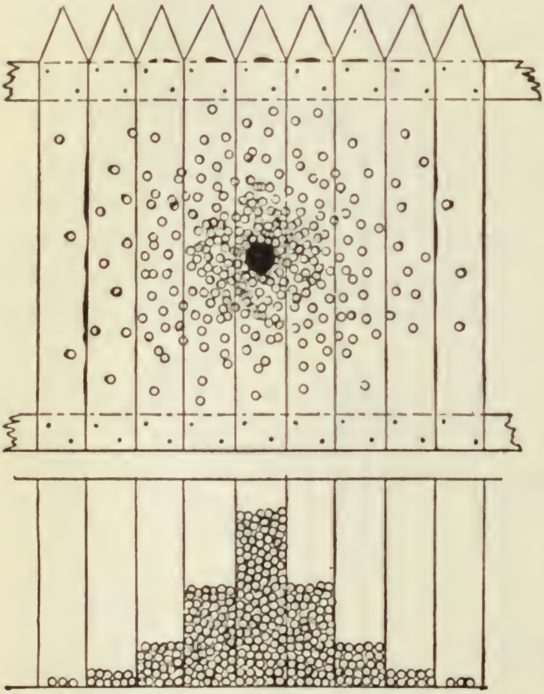
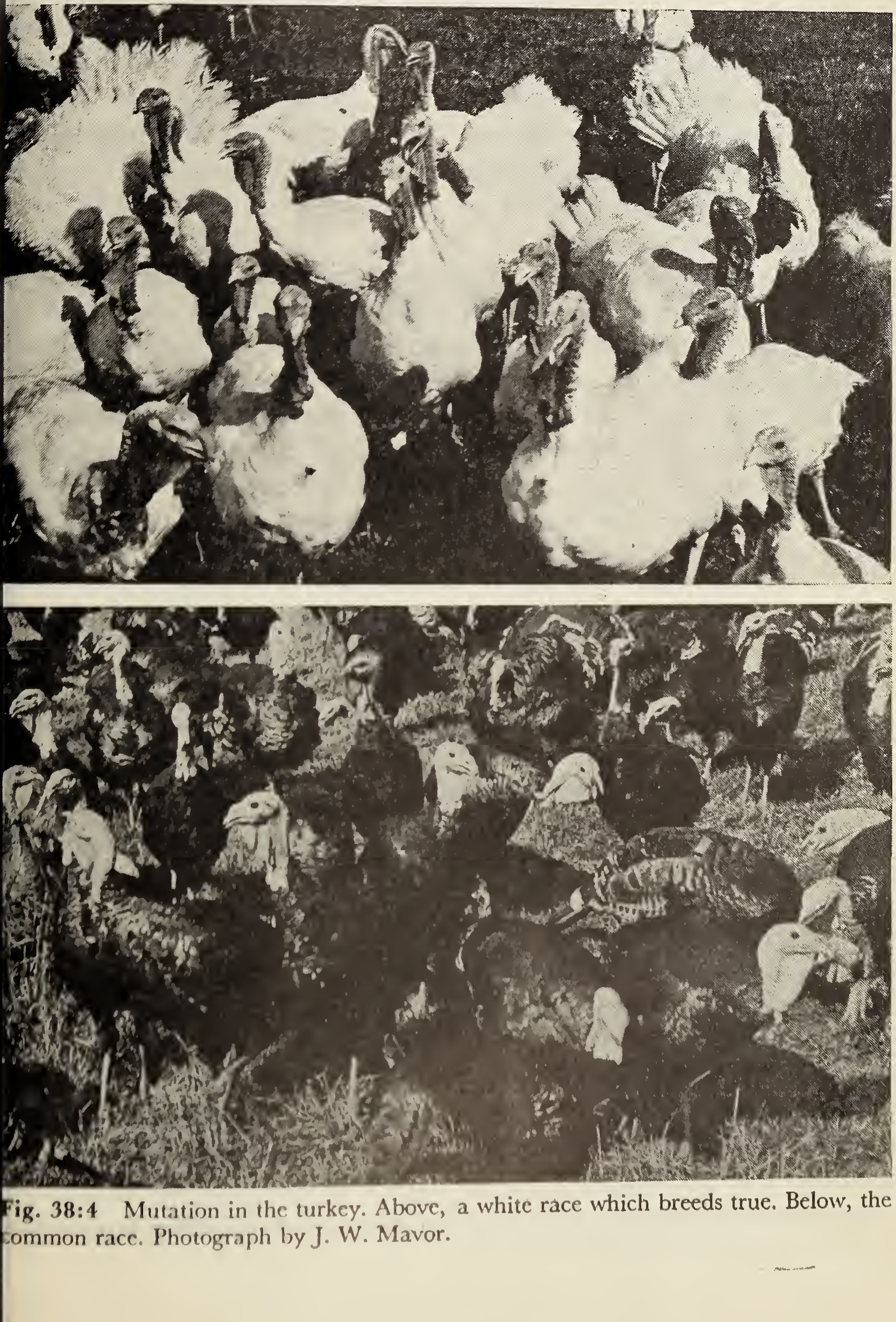


Fig. 38:3 When deviations in all directions are equally probable, as in the case of shots fired at a target by an expert marksman, the "frequencies" will arrange themselves in the manner shown by the bullets in the compartments above. A line drawn along the tops of these columns of bullets would form a "normal probability curve." Diagram by C. H. Popenoe. From Popenoe and Johnson, *Applied Eugenics,* The Macmillan Company.

A similar diagram can be made from the measurement of the distances of the shots of an expert marksman from the center of the target. The diagram will be found to be on the whole similar to that obtained from the measurements of the recruits (Fig. 38:3). If, in the two diagrams, the tops of the columns representing the different heights are joined, a **distribution curve** is obtained. The curve for the distances from the target represents a distribution which is entirely due to chance and s called a **probability curve.** The distribution curve for the recruits hows that it also corresponds approximately to a probability curve.

Not all biological characters when measured in a sample of a popula-ion give a probability curve. This is explained as being due to the fact hat in such cases some factor at work upsets the even distribution.



ig. 38:4 Mutation in the turkey. Above, a white race which breeds true. Below, the ommon race. Photograph by J. W. Mavor.

B. MUTATIONS

Among a flock of purebred sheep on a farm in New England there appeared about one hundred years ago a lamb with very short, bowed legs. The lamb was reared and bred and gave rise to the Ancon breed of sheep, a breed with short, bowed legs. The different breeds of hornless cattle have originated in the same way from a mutation which first appeared in a single individual. Another example is that of the white turkeys now popular with breeders (Fig. 38:4). A **mutation** may be defined as an abrupt heritable modification of a character or group of characters of an organism. Mutations are due to changes in the germ plasm or hereditary material. Many examples of mutations will be given in subsequent sections.

Extensive investigations in experimental breeding have established that mutations may be due to changes in the number of chromosomes, in the chromosomes themselves, or in the genes which they contain (gene-mutations). Exceptions occur in plants in which some characters have been shown to be carried in the cytoplasm. The characteristic which is called a mutation, for example the short legs of the sheep referred to, is, in fact, but the final phase of a complicated process which had its origin in a change in a gene in one of the chromosomes in one of the germ cells of one of the normal ancestors of the sheep. Thus the study of heredity leads to the conclusion that every animal and plant has an assortment of genes in its chromosomes which are responsible for its various inherited characteristics.

4. HOW MUTATIONS ARE INHERITED

A. A SIMPLE OR MONOHYBRID CROSS

When mutations occur among our domesticated plants and animals they are often preserved by inbreeding and selection. It is in this way that most of our fancy breeds and garden flowers have arisen.

For the purpose of studying the inheritance of mutations we will take as an example two varieties of snapdragon, one of which has red flowers, the other white flowers. These breed true from seed. Let us now cross a plant of the red-flowered variety with one of the white-flowered variety (Fig. 38:5). These two plants may be called the **parents** and designated by the letter P. The seeds which are formed give rise to the **first generation of offspring,** F_1. These plants all have pink flowers. If now these F_1 plants are self-fertilized, i.e., the stigmas of the flowers of each plant allowed to receive pollen only from the same plant, the **offspring of the**

second generation, F_2, are found to consist of three kinds of plants, viz., plants with red flowers, plants with pink flowers, and plants with white flowers, and these are found to be in the proportion of one red-flowering to two pink-flowering to one white-flowering plant. This experiment has been performed over and over again; the result is fact, not theory.

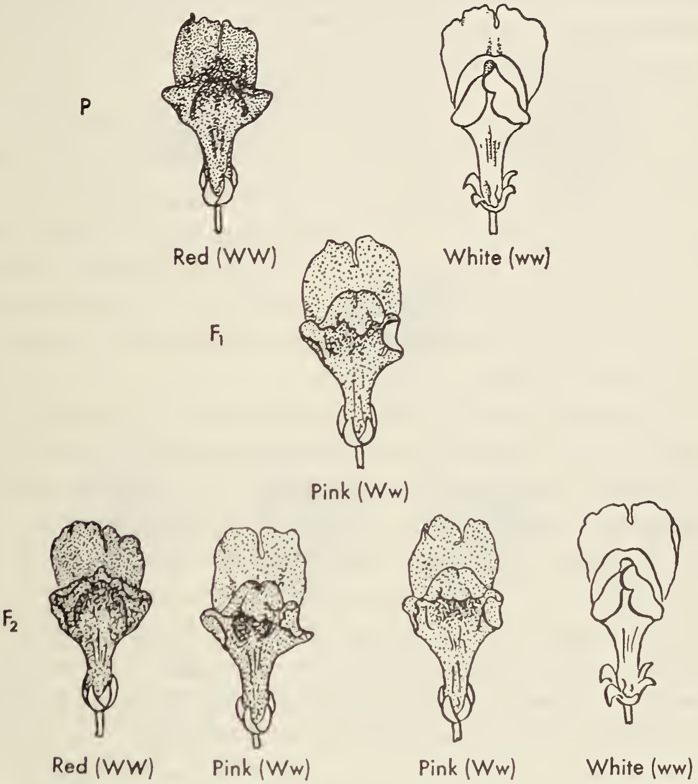


Fig. 38:5 Diagram representing a cross between a pure red and a pure white snapdragon. The F_1 are all pink. The F_2 consist of red, pink, and white individuals in the proportion of one red to two pink, and one white. (Actually, in the original experiments on inheritance in these plants in Germany, plants with ivory rather than white flowers were used.) The shape of the flowers is not involved.

The explanation of this peculiar phenomenon is to be found by relating the characters to their genes. The cells of the red-flowering snapdragon contain the gene in the condition which leads to the production of red flowers, those of the white-flowering snapdragon contain it in the condition which leads to the production of white flowers. Let us designate these two conditions by W, and w, respectively, and let us further assume that in each case the genes are in each of a pair of autosomes. Disregarding the other genes and chromosomes we designate the genetic composition of the cells of the red-flowered snapdragon by WW, and those of the white-flowering plant by ww.

When the haploid microspores are formed in the pollen sacs of the red-flowered parents, P, they will contain only one of a pair of homologous chromosomes and therefore only one of the genes. Their genetic composition will be designated by W. The same will be true of the megaspores formed in the ovules and they will also have the genetic composition W. Similarly the microspores of the white-flowered plants will have the genetic composition w and the megaspores also w.

When the two varieties are crossed and an egg in the embryo sac of a red-flowered plant, P, is fertilized by the sperm nucleus from the pollen of one of the white-flowered plants, P, the resulting zygote, F_1, will have the genetic composition Ww. This zygote gives rise to a plant which has pink flowers. Evidently neither of the two genes has had matters all its own way and an intermediate color is produced. The same result occurs when an egg from a white-flowered plant is fertilized by a sperm nucleus from a red-flowered plant.

The microspores formed by the pink-flowered, F_1, plants are of two kinds, since the two homologous chromosomes separate during meiosis and go with their genes to different spores. The genetic constitution of these two kinds of spores will be W and w. The megaspores are also of the same two kinds, W and w. Thus equal numbers of two kinds of female gametophytes or embryo sacs and equal numbers of two kinds of male gametophytes or pollen tubes are formed by the F_1 plants. Either kind of pollen tube may grow down to either kind of embryo sac and either kind of egg has an equal chance of being fertilized by either kind of sperm nucleus. Thus four different combinations are possible and occur on the average in equal proportions: a W containing sperm nucleus with a W containing egg, giving rise to a WW zygote; a W containing sperm nucleus with a w containing egg, giving a Ww zygote; a w containing sperm nucleus with a W containing egg, giving another Ww zygote; and lastly a w containing sperm nucleus with a w containing egg, giving a ww zygote. It is clear that in the F_2 plants the WW zygotes give rise to the red-flowered, the Ww and wW to the pink-flowered, and the ww to the white-flowered plants. It is also clear that the genetic explanation calls for their occurrence in the same proportion as was found in the experiment.

Certain special terms are used to define the different kinds of individuals of the different generations in the above experiment. The parents, P, which breed true and have the gene in question in the same condition in each chromosome of the homologous pair in which it occurs are said to be **homozygous.** The immediate offspring of these parents, F_1, which possess the gene in the condition to produce red flowers in one chromosome and in the condition to produce white flowers in the other chromosome and do not breed true are said to be **heterozygous.** The second generation of offspring, F_2, contains both homozygous and heterozygous individuals.

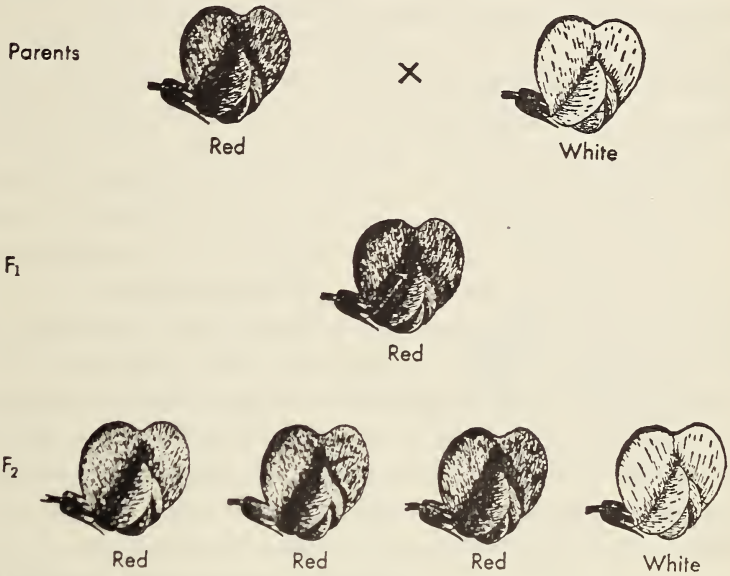


Fig. 38:6 Cross between a pure red-flowered and a pure white-flowered pea plant, showing the dominance of red flower color in the F_1. If an F_1 plant is self-fertilized, the resulting F_2 generation is three-fourths red-flowered and one-fourth white-flowered. From Sinnott and Dunn, *Principles of Genetics*, by permission of the McGraw-Hill Book Company.

The hereditary characteristics, red flowers and white flowers, are passed from one generation to another intact. Thus the red-flowered character of one of the parents appears again in the F_2 as a red-flowered character unaffected by the cross and its disappearance in the F_1. Such characters are called **unit characters** or **Mendelian characters** after the name of their discoverer, Gregor Mendel. The fact that the characters red-flowered and white-flowered, although lost from sight in the F_1 generation, reappear in separate individuals in the F_2 is expressed by the term **segregation.**

In the example chosen the F_1 individuals were unlike either parent. In fact as far as the color of their flowers was concerned, the character considered, they were intermediate. It is, on the whole, rather exceptional for Mendelian characters to behave in this manner. More usually the F_1 individuals are like one of the parents. To illustrate this we may take as an example two similar varieties of the pea plant. If a purebred red-flowered plant of the pea be crossed with a purebred white-flowered plant, the F_1 will all be red-flowered (Fig. 38:6). If an F_1 plant is self-fertilized it will give rise to red-flowered and white-flowered plants in the proportion of three to one. In this case it is clear that the heterozygous plants of the F_1 and F_2 generations, instead of being pink as in the case of the snapdragon, are red like the purebred parent. Thus in the pea, when one of the chromosomes contains the gene in the condition to produce red flowers and the other homologous chromosome contains it in the condition to produce white flowers, the resulting flowers are red. When this occurs the red-flower character is said to be **dominant,** and the white-flower character **recessive.** In the pea plant, therefore, red-flower character is dominant to white-flower character. In the snapdragon the same characters show incomplete or **partial dominance.**

It will have become apparent that it is not always possible to tell the genetic composition of an individual, i.e., the condition of its genes from its appearance. Individuals which appear alike but may not have the same genetic composition are said to be of the same **phenotype.** Individuals which have the same genetic composition are said to be of the same **genotype.** Thus in the first cross considered, that between a red-flowered and a white-flowered snapdragon, there were two phenotypes among the parents, i.e., a red-flowered plant and a white-flowered plant, one phenotype in the F_1, i.e., pink, and three different phenotypes among the F_2. In this case the phenotypes were also genotypes. In the cross between the red-flowered and white-flowered pea plants but two different phenotypes appeared since the individuals which are heterozygous for the two characters are red-flowered and exactly like the homozygous red-flowered plants. There are, however, as in the other cross three genotypes, plants homozygous for the red-flowered character, plants homozygous for the white-flowered character, and plants heterozygous for the red-flowered and white-flowered characters.

Characters which, like red-flower color and white-flower color in the experiments, are alternatives and mutually exclusive in their expression, are said to be **allelomorphs** or **alleles.** Allelomorphic characters are due to different conditions of the same gene. The term is also applied to the gene. Thus the gene in the condition to cause the production of red flowers is the allelomorph of the same gene in the condition to produce white flowers.

B. THE BACKCROSS

The term **backcross** is applied to a cross between one of the F_1 individuals and the parent individual with the recessive character. Thus in the case of the snapdragon this would mean the crossing of a pink-flowered individual, heterozygous for red-flower color and white-flower color, with a white-flowered individual homozygous for the white-flower color. The result of such a cross is shown in the diagram (Fig. 38:7). The F_1 of such a cross contain pink-flowered and white-flowered individuals in equal numbers.

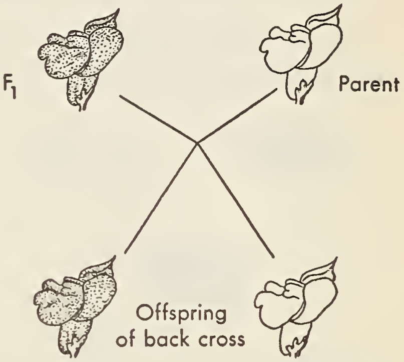


Fig. 38:7 A backcross. A pink F_1 snapdragon, upper left, is crossed with its recessive (white) parent, upper right, and gives rise to pink-flowering and white-flowering plants in equal numbers.

The reason for this is clear when the genetic constitution of the individuals and the distribution of the genes to the gametes is considered. The pink-flowered individual being heterozygous produces two kinds of megaspores and two kinds of pollen and, therefore, two kinds of eggs and two kinds of sperms. In one kind the gene is in the condition to produce red flowers, in the other kind it is in the condition tending to produce white flowers. The two kinds of megaspores occur in equal proportions and equal numbers of the two kinds of eggs are produced. In the same way two kinds of sperm nuclei are formed. The white-flowered plant being homozygous produces only one kind of megaspore and one kind of pollen and hence only one kind of egg and one kind of sperm nucleus. In these the gene is in the condition tending to produce white flowers. When an egg from the embryo sac of a pink-flowered plant containing the gene in the condition which tends to produce red flowers is fertilized by a sperm nucleus from the pollen tube of the white-flowered plant the zygote is heterozygous and produces pink flowers. When a similar egg containing the gene in the condition tending to produce white flowers is fertilized by a sperm nucleus from a pollen tube of the white-flowered plant the zygote is homozygous and produces white flowers. The same explanation applies when an egg of the white-flowered plant is fertilized by either of the two kinds of sperm nuclei produced by the heterozygous pink-flowered plant.

The backcross is useful in experimental breeding because it makes possible the testing of individuals which are alike as to phenotype but which may differ as to genotype. Thus the red-flowered individuals of the F_2 in the cross involving the pea plant could be tested by backcrossing to white-flowered plants, when approximately two out of every three of these F_2 would be found to be heterozygous and produce white-flowered and red-flowered plants in equal numbers.

C. A CROSS INVOLVING FREE ASSORTMENT

For the sake of variety we will choose our next example from the animal kingdom. In guinea pigs rough hair is dominant to smooth hair and black coat color to white coat color. If a smooth black guinea pig is crossed with a rough white guinea pig the F_1 are all rough and black, these being the two dominant characters (Fig. 38:8). When these individuals are crossed the F_2 consist of four phenotypes which occur in the following proportions:

Rough black	9
Rough white	3
Smooth black	3
Smooth white	1

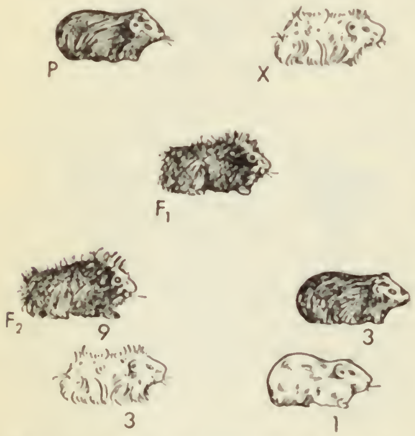


Fig. 38:8 Cross between a smooth, black and a rough, white guinea pig. The F_1 are rough, black and when interbred produce four kinds of offspring in the proportions: 9 black, rough, 3 black, smooth, 3 white, rough, and 1 white, smooth. After W. E. Castle.

This assortment can be explained if the gene which determines white or black color is in a different chromosome from the gene which determines rough or smooth hair. According to the method of notation we have employed, the character rough and the gene in the corresponding condition may be designated by R, and the allelomorphic character smooth and the corresponding condition of the gene by r. Similarly B and b may denote black and white coat color respectively. The genetic composition of the smooth black parent may then be expressed as rrBB, and that of the rough white parent as RRbb (Fig. 38:9). The gametes produced by the smooth black guinea pig will be alike and will contain one chromosome of each of the two pairs. They will be denoted by rB. The gametes of the other parent will similarly be denoted by Rb. The F_1 individuals which are rough black and phenotypically and genotypically alike, have the genetic composition RrBb. Each of these F_1 individuals produces four kinds of gametes in equal proportions, viz., RB, rB, Rb, and rb (Fig. 38:9). Any one of the four kinds of gametes from one parent has an equal chance to unite with any one of the four kinds of gametes of the other parent. Thus sixteen combinations are equally probable. These are shown in diagrammatic form on a checkerboard with four squares on a side (Fig. 38:10). A study of this diagram shows that in the F_2 there are nine different genotypes, i.e., there are nine different kinds of individuals when the F_2 are classified according to their genetic composition. On the other hand, as the result of the experiment shows, there are only four different phenotypes, that is, there are only four different kinds of individuals when the F_2 are classified according to their visible characters. The different kinds of F_2 individuals are listed in Table 38:1. This table shows that the proportion in which the four phenotypes occur is 9 : 3 : 3 : 1, that is, out of every sixteen individuals nine have both dominant characters, in this case rough and black; three have one dominant character and one recessive character; and three have the other dom-

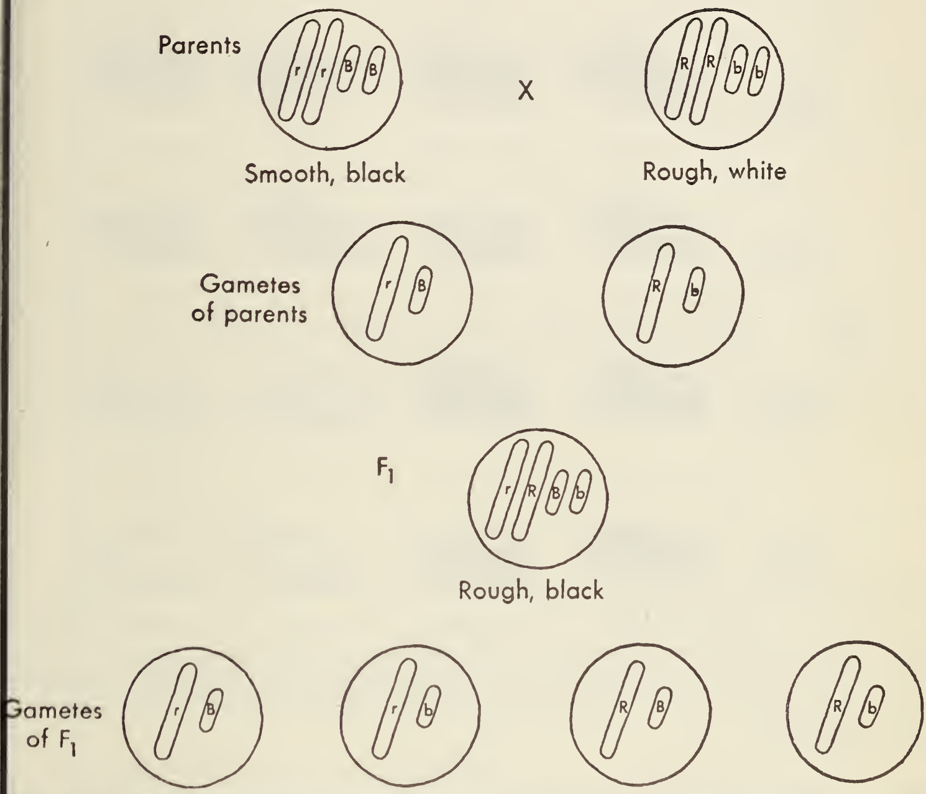


Fig. 38:9 Behavior of the chromosomes in a cross between a smooth, black and a rough, white guinea pig. B, black gene; b, white gene; R, rough gene; r, smooth gene.

inant character and the other recessive character, while only one individual has both the recessive characters. It should be remembered that the proportions stated above will only be found when there is independent or free assortment, i.e., when the two genes involved are in different chromosomes.

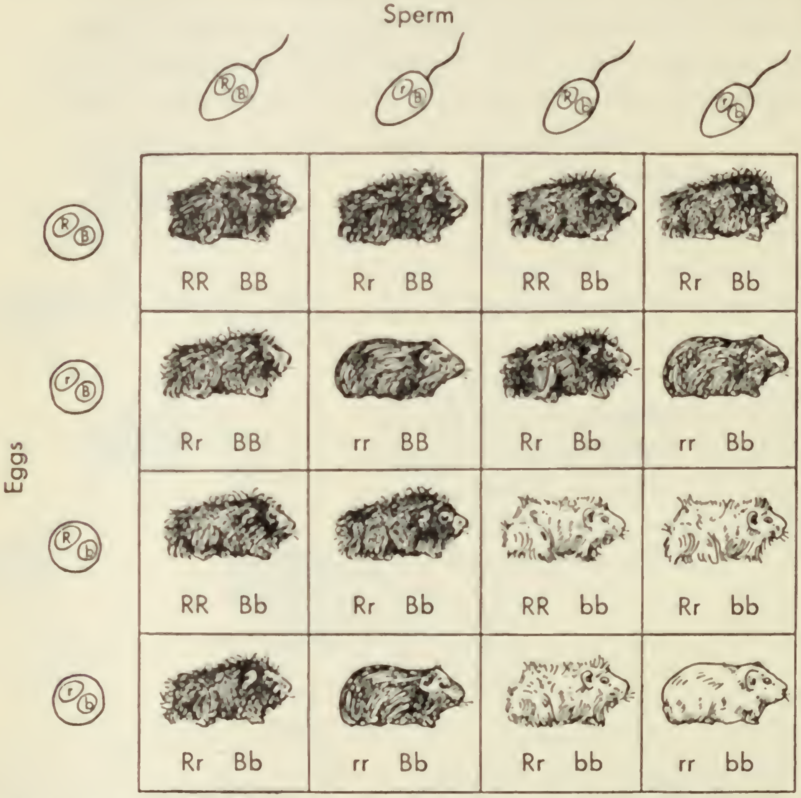


Fig. 38:10 Diagram showing the phenotypes and genotypes occurring in a cross between two guinea pigs, both heterozygous for the characters rough and smooth, and black and white.

TABLE 38:1. PHENOTYPES AND GENOTYPES IN THE F_2 OF A CROSS BETWEEN A SMOOTH BLACK AND A ROUGH WHITE GUINEA PIG

PHENOTYPES	NUMBER	GENOTYPES	NUMBER
Rough black	9	RRBB	1
		RrBB	2
		RRBb	2
		RrBb	4
Smooth black	3	rrBB	1
		rrBb	2
Rough white	3	RRbb	1
		Rrbb	2
Smooth white	1	rrbb	1

Cases occur in which three or more genes in three or more different chromosomes appear in a cross and show the same kind of independent assortment as illustrated in the above example. Such cases can be worked out by the same method. When three genes are involved the checkerboard will contain eight squares on a side. When four are involved there will be sixteen squares on a side, and so on.

Sometimes what appears to be a relatively simple character in the phenotype involves a number of genes and is really the combination of a number of genetic factors then called **multiple factors.** This, for example, has been found to be the case with skin color in man. Investigations indicate that the dark color of a "full-blooded negro" is the result of a number, perhaps five or six, of partially dominant factors, which are independently inherited like the characters rough and black in guinea pigs. When a cross occurs between a negro and a white person the genes become separated as in the case of the guinea pig so that different degrees of color occur, depending on the number of dominant and recessive factors present. Thus the darkest individuals would occur when all of the factors were represented by dominants and the lightest individuals (white) when all the factors were represented by recessives. Both extremes would, however, be rare.

D. MENDELISM

The experimental results described in the two previous sections have been found to apply to a large number of hereditary characters in many different species of plants and animals. They may be stated in the form of four principles or laws as follows:

(1) PRINCIPLE OF UNIT CHARACTERS

This principle asserts that certain hereditary characters, in fact all the hereditary characters about the transmission of which we have certain information, behave as units and are passed from one generation to another as such.

(2) PRINCIPLE OF DOMINANCE AND RECESSIVENESS

This principle, illustrated in the crossings involving the garden pea and guinea pigs, is now known not to apply to all crosses or characters, as illustrated by the snapdragon. According to it, in a cross involving a dominant character and its recessive allelomorph, only the dominant character appears in the F_1.

(3) PRINCIPLE OF SEGREGATION

This principle asserts that characters, like white in the examples above, may go into a cross, disappear in the F_1, and appear in their original form in later generations, apparently unaffected by their submergence.

(4) PRINCIPLE OF FREE ASSORTMENT

According to this principle certain characters such as rough hair and black coat color behave quite independently in inheritance.

These four principles were first discovered by Gregor Mendel, an Austrian monk, as a result of experiments on plants in the garden of his monastery. The experiments were begun in 1857 and the results published by him in 1866. The work of Mendel marks the beginning of the modern scientific study of heredity. For this reason the study and application of these principles is often called **Mendelism.** His paper remained almost unnoticed by biologists until 1900, when the great significance and wide application of his results were recognized. Mendel's success in discovering what are now regarded as the fundamental laws of heredity was largely due to his insight in choosing for his experiments certain definite characters and following them individually through successive generations of offspring and analyzing the results.

E. LINKAGE AND CROSSING OVER

Free assortment, we have shown, occurs when the genes concerned are in different chromosomes. When the genes are in the same chromosome another phenomenon called **linkage** occurs. Let us suppose, for example, that in the cross involving a smooth black and a rough white guinea pig the gene which by its condition determined whether the individual was to be smooth or rough was in the same chromosome as the gene which determined the characters black and white. If the genes always stayed in this chromosome it is clear that a smooth guinea pig would always be black and a white guinea pig would always be rough. The linkage in this case would be complete. It has been shown by breeding that there are pairs and in some cases whole groups of characters which, when brought together in crosses, do not show free assortment and on the other hand do not show complete linkage. This is explained by assuming that an interchange of corresponding parts between two chromosomes may occur, probably during or soon after synapsis. This is called **crossing over.** Thus if two homologous chromosomes contained a series of genes, a, b, c, d, e, f, g, and a′, b′, c′, d′, e′, f′, g′, arranged along their length, there might be an interchange such that the part of one containing c′, d′ was interchanged with the part of the other containing c, d. In this way the genes which determined characters showing linkage would be separated. There is microscopical evidence that in certain cases crossing over, with its attendant separation of the genes, occurs.

The study of linkage combined with microscopic studies on chromosomes has led to the location of the genes in the chromosomes of certain species, notably the fruit fly, *Drosophila*, and the corn plant, *Zea mays*. It is beyond the scope of this text to go into the methods by which such locations of genes are determined. It may be said, however, that the evidence shows that there is a linear arrangement of the genes in the chromosomes. That is, the genes in any one chromosome are arranged in a series along a line extending from one end of the chromosome to the other end.

F. SEX–LINKED CHARACTERS

Sexual characters or the characters which distinguish the sexes should be clearly distinguished from sex-linked characters. The sex of an individual seems to depend not on a single gene or group of genes but on the number of X-chromosomes which its soma cells possess. Thus an individual with two X-chromosomes is a female, while an individual with one X-chromosome is a male. A sex-linked character may have little to do with any of the characters which distinguish the sexes and may be possessed by either sex. A character is called sex-linked when its gene is carried in the X-chromosome. The inheritance of a sex-linked character does not follow the pattern described for the inheritance of a simple cross involving a character having its gene located in an autosome.

Let us take first the case of a white-eyed female crossed with a red-eyed male drosophila (Fig. 38:11). The F_1 females are all red-eyed while the F_1 males are all white-eyed, a condition exactly the opposite of that of the parents. If now one of the red-eyed F_1 females is mated to a white-eyed F_1 male there will arise four kinds of F_2 flies in equal proportions, viz., white-eyed females, red-eyed females, white-eyed males, and red-eyed males.

The explanation of this is obtained by assuming that the gene which determines whether the eyes shall be red or white is located in the X-chromosome and passes with it in inheritance. The white-eyed female parent contains in each of her cells two X-chromosomes each of which contains the gene in the condition to produce white eyes. She is homozygous for the recessive character and her genetic constitution may be represented by ww. Each of her eggs contains a single X-chromosome and has one gene in the condition to produce white eyes. The red-eyed male parent has in each of his cells only a single X-chromosome which contains the gene in the condition to produce red eyes. His genetic constitution may be represented by W. The sperms which he produces are of two kinds, one kind contain the X-chromosome and therefore the gene in the condition to produce red eyes, and the other kind contain the Y-chromosome and are without the gene in question. When an egg from the female parent is fertilized by one of the first named kind of sperms, i.e., one containing W, there results a zygote with two X-chromosomes in each of its cells, one coming from the mother and containing the gene in the condition to produce white eyes, and the other coming

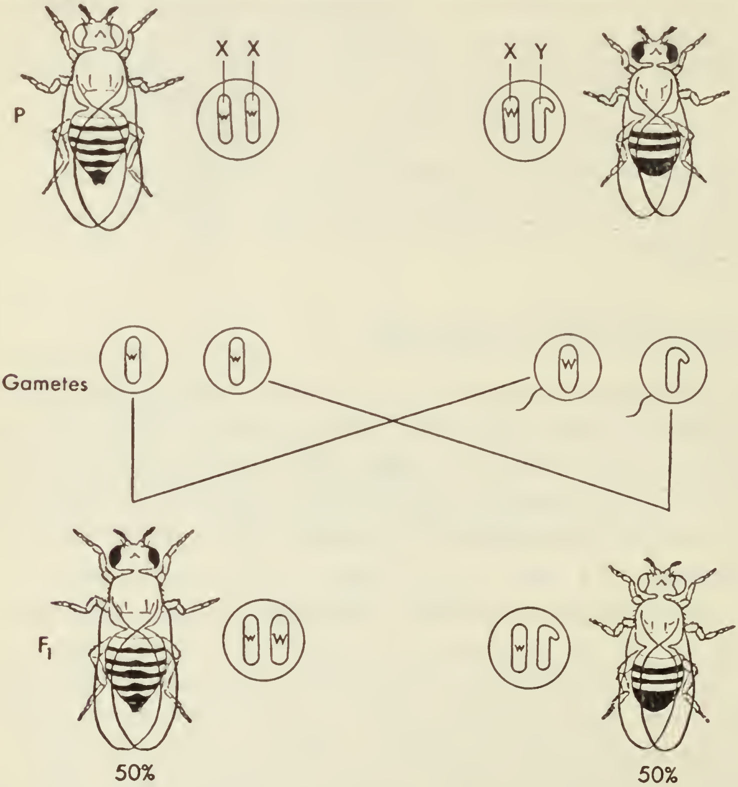


Fig. 38:11 Diagram illustrating a cross between a white-eyed female and a red-eyed male fruit fly (*Drosophila*). Each of the eggs contains the gene in the condition to produce white eyes. The sperms are of two kinds in equal numbers. One kind contain an X-chromosome and the gene in the condition to produce red eyes. The other kind contain a Y-chromosome and lack the gene. Any egg has an equal chance of being fertilized by a sperm of either kind. The female F_1 are all red-eyed and heterozygous for this character, while the male F_1 are all white-eyed since the single X-chromosome which their cells contain came from their mother and contains the gene in the condition to produce white eyes.

from the father and containing it in the condition to produce red eyes. This zygote is heterozygous, Ww, for the eye colors in question but it is phenotypically red-eyed. When, on the other hand, an egg from the female parent is fertilized by a sperm containing a Y-chromosome, there results a zygote with one X-chromosome and one Y-chromosome in each of its cells, the X-chromosome coming from the mother and containing the gene in the condition to produce white eyes. These individuals are males and have white eyes.

Coming now to the crossing of the F_1 individuals, the heterozygous red-eyed females, Ww, produce two kinds of eggs. In one kind the gene is in the condition to produce red eyes, W; in the other in the condition to produce white eyes, w. The white-eyed males produce two kinds of sperms. In the sperms containing the X-chromosome, the gene is in the condition to produce white eyes, w; in the sperms containing the Y-chromosome it is absent. When two of the F_1 are crossed four combinations are possible and have an equal chance of occurring. An egg containing the gene in the condition to produce white eyes, w, when fertilized by a sperm with an X-chromosome containing the gene in the condition to produce white eyes gives rise to a homozygous white-eyed female, ww. The same kind of egg fertilized by a sperm with a Y-chromosome gives rise to a white-eyed male, w. An egg containing the gene in the condition to produce red eyes, W, when fertilized by a sperm with an X-chromosome containing the gene in the condition to produce white eyes, w, gives rise to a heterozygous red-eyed female, Ww. A similar egg when fertilized by a sperm containing a Y-chromosome gives rise to a red-eyed male, W.

It has probably become evident from the above discussion that in the case of sex-linked inheritance the sons, since they obtain their X-chromosome from their mother, always inherit their sex-linked characters from her, while the daughters which obtain one X-chromosome from each parent inherit their sex-linked characters equally from both parents.

The reciprocal cross, i.e., that of a homozygous red-eyed female with a white-eyed male gives a different result both in the F_1 and the F_2. By a method similar to that used above and the application of the same principles the results of such a cross can be predicted and explained. This is the subject of a problem at the end of this chapter.

G. LETHAL MUTATIONS

It is not surprising that some mutations are incompatible with the life of the individual which might develop. Such mutations are called **lethal**

mutations. It has been found that such mutations are more frequent in their occurrence than visible mutations. One may ask how the existence of such mutations can be determined since by definition an individual with the mutation cannot survive. The method depends on the use of linkage. To take a simple example, suppose that a lethal mutation occurred in the X-chromosome of a fly near the gene for white eye and therefore closely linked with it. Suppose further that the gene was lethal only when homozygous. Then if the mutation occurred in one of the eggs of a white-eyed female, which was fertilized by a red-eyed male, the offspring would be viable since the lethal mutation is present only in one of the X-chromosomes. Now suppose that this fly which would be heterozygous for white eye and the lethal mutation is mated to a normal red-eyed fly. The expectation from such a cross would be approximately 50 per cent red-eyed females, 25 per cent red-eyed males, and 25 per cent white-eyed males were it not for the presence of the lethal mutation (Fig. 38:12). Since the white-eyed males would contain the lethal mutation without its normal allelomorph these flies do not appear and the lethal mutation is demonstrated.

Parents		$\frac{WL}{wl}$	×	$\frac{WL}{Y}$	
Gametes	WL	wl		WL	Y
F_1	$\frac{WL}{WL}$	$\frac{WL}{Y}$		$\frac{wl}{WL}$	$\frac{wl}{Y}$
	Red-eyed ♀	Red-eyed ♂		Red-eyed ♀	Die
	25%	25%		25%	25%

W = red eyed, w = white eyed, L = normal, l = lethal, Y = Y-chromosome.

Fig. 38:12 Demonstration of a lethal mutation. The horizontal lines between the symbols are used to indicate that the genes on the same side of them are in the same chromosome. The female parent is heterozygous for white eye-color and for the lethal. The male parent is normal for both these characters.

5. SOME MENDELIAN CHARACTERS

Thousands of hereditary characters have been followed in breeding experiments or in recorded pedigrees and found to conform to Mendel's laws. Table 38:2 gives a few examples. It will be noticed that the normal allelomorph, which is the character usually found in the wild animal or plant, or the character usually present in the common cultivated variety, is usually, but not always, dominant. A character such as the color of the flowers may behave in one way in one species of plant and in another way in a different species. There is no way known of predicting how a given new character will behave in a cross until it has been bred.

TABLE 38:2. SOME MENDELIAN CHARACTERS

ORGANISM	DOMINANT OR PARTIALLY DOMINANT CHARACTER	RECESSIVE CHARACTER
Garden pea	Red flowers	White flowers
	Yellow seeds	Green seeds
	Smooth seeds	Wrinkled seeds
Snapdragon	Red flowers	White flowers
Indian corn	Yellow endosperm in seed	White endosperm in seed
	Starchy endosperm	Sweet endosperm
Fruit fly (*Drosophila*)	Gray body	Ebony body
	Long wings	Vestigial wings
Guinea pig	Rough coat	Smooth coat
	Black coat	White coat
	Short hair	Long hair

6. KINDS OF CHANGES IN THE GERM PLASM

A. *CHANGES INVOLVING ENTIRE CHROMOSOMES*

According to our definition a mutation is a character which arises suddenly and behaves as a unit character in heredity. So far we have discussed only gene mutations, i.e., mutations due to changes in a single gene. Other changes are known to occur in the germ plasm (Fig. 38:13).

POLYPLOIDY. In most species of plants and animals the nuclei of normal individuals contain the diploid or $2n$ assortment of chromosomes. Not infrequently in plants, more rarely in animals, individuals are observed the nuclei of which contain in addition to the diploid set of chromosomes one or more entire haploid sets. When there is one additional haploid set of chromosomes, the nuclei having then the $3n$ chromosome condition, the individual is called a **triploid.** When two complete haploid groups of chromosomes are added, giving a nucleus with a $4n$ assortment of chromosomes, the individual is called a **tetraploid.** Tetraploid individuals are usually larger and have larger cells and larger nuclei than normal diploid individuals. Higher multiples of the normal $2n$ condition may occur and individuals with the $6n$ and even $8n$ condition have been observed. Such individuals are called **polyploids.** In some cases, the differences between allied species seem to depend, at least in part, on a multiplication of chromosome groups. Thus species of wheat are known in which the numbers of chromosomes in the gametophyte (haploid) generations are 7, 14, and 21 respectively, corresponding to 14, 28, and 42 for the sporophyte (diploid) generation.

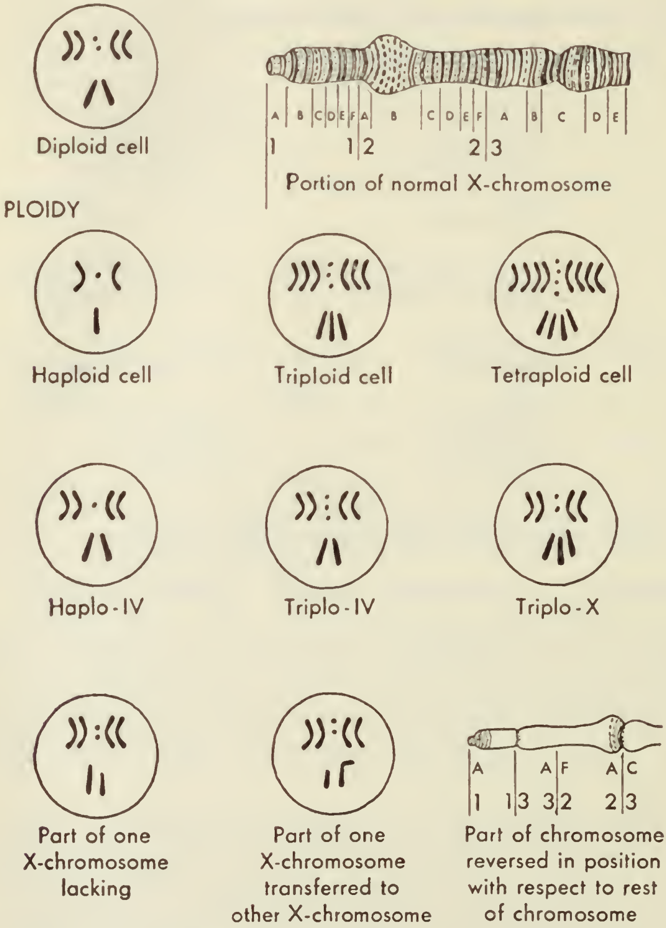

Diploid cell
A B C D E F A B C D E F A B C D E
1 1 2 2 3
Portion of normal X-chromosome
PLOIDY
Haploid cell
Triploid cell
Tetraploid cell
Haplo-IV
Triplo-IV
Triplo-X
Part of one X-chromosome lacking
Part of one X-chromosome transferred to other X-chromosome
A A F A C
1 1 3 3 2 2 3
Part of chromosome reversed in position with respect to rest of chromosome

Fig. 38:13 Types of chromosome changes giving rise to mutations. The portion of a normal X-chromosome is redrawn after Painter in the *Journal of Heredity* by permission.

More rarely there are animals, and plants in the sporophyte generation, the nuclei of which contain only the haploid (n) chromosome assortment. Such individuals are called **haploids.** This happens normally in the case of the male bee or drone. Such individuals carry only a single set of genes which they usually transmit intact in their eggs or sperms.

HETEROPLOIDY. In place of a whole set of chromosomes, a single chromosome or a part of a set may be added to or subtracted from the normal diploid assortment. This condition is called **heteroploidy.** It is caused by the failure of homologous chromosomes to separate in reduction. This failure to separate is called **nondisjunction.** The occurrence of a certain type of individual in breeding experiments in the fruit fly, *Drosophila*, were believed to indicate nondisjunction of the X-chromosome. Cytological examination of these individuals confirmed the hypothesis and at the same time provided one of the most convincing proofs that the chromosomes are the bearers of hereditary characters. Normally, as described in the section on sex-linked characters, when a white-eyed female drosophila is mated to a red-eyed male the offspring of the first generation consist of equal numbers of red-eyed females and white-eyed males, since the gene for this eye color is carried in the X-chromosome and the males get their single X-chromosome from their white-eyed mothers and the daughters get one of their X-chromosomes from their fathers and this X-chromosome has the gene in dominant condition which produces red-eyes. However, very rarely an "exceptional" red-eyed son or white-eyed daughter occurs. This is explained if, during the maturation process in the mother, two X-chromosomes stayed together giving rise to an egg which contained either two X-chromosomes or no X-chromosome. When an egg containing two X-chromosomes is fertilized by a sperm containing a Y-chromosome, the resulting female, which has the formula XXY, is white-eyed because she got both her X-chromosomes from her white-eyed mother. When an egg containing no X-chromosome is fertilized by a sperm containing an X-chromosome the resulting individual which has the formula X is a male and red-eyed because he got his chromosome from his father instead of, as would normally occur, from his mother.

B. CHANGES WITHIN THE CHROMOSOMES NOT INVOLVING CHANGES IN THE INDIVIDUAL GENES

DEFICIENCY. A chromosome may become broken and a part lost. This gives rise to what is known as a *deficiency*, in which one gene or a group of genes are absent from the chromosome in question. An example is found in the mutation called Notch in *Drosophila*. This mutation is not due to a change in a gene but to a deficiency in the X-chromosome which involves a number of genes.

TRANSLOCATION. In place of a part of a chromosome being lost, the part may be transferred and become attached to another chromosome in the same nucleus. This is known as *translocation*. A translocation may take place in the form of a reciprocal exchange of parts between two nonhomologous chromosomes (not to be confused with the reciprocal change between homologous chromosomes which occurs in crossing over), or the part may become attached to another intact chromosome.

INVERSION. This occurs when a chromosome is broken and the parts come together again so that the ends are inverted. In this case the order in which the genes are arranged in the chromosome is changed. Such a condition gives rise to changes in crossing over.

C. CHANGES IN THE GENES

Probably the most important changes in the germ plasm are those which occur within the genes. Such changes are called **gene-mutations.** They produce alleles or allelomorphic genes. Since many genes can change in more than one way multiple alleles are produced. Thus in *Drosophila* there is a series of allelomorphic eye-colors determined by a series of multiple alleles. Multiple alleles are not to be confused with multiple factors which are represented by different genes and can coexist in an individual. Although such changes have been frequently demonstrated in breeding experiments, the study of the nucleus and its contained chromosomes has so far not yet reached the stage when individual genes can be identified under the microscope. It is, therefore, as yet not possible to describe even in the most general terms the actual changes which occur in the gene.

7. MUTATION, NATURAL AND ARTIFICIAL

A. NATURAL MUTATIONS

Practically, new mutations come to light very seldom. In the very intensive study of the fruit fly, *Drosophila*, some 25,000,000 or 30,000,000 individuals have been examined critically and about 500 gene mutations have been identified. Undoubtedly many mutations escaped observation, probably a greater number than were actually observed. The rate for certain individual mutations has been determined approximately. Thus for the mutation from the normal red eye color to white eye color the rate is about 1 per 1,000,000, which means that the mutation occurs on the average in one out of every million germ cells. This and many other mutations have occurred over and over again. This would seem to indicate that although multiple alleles do occur any individual gene can undergo at most only a few different mutations.

B. MUTATIONS ARTIFICIALLY PRODUCED

The first changes in the germ plasm to be produced artificially, propagated by experimental breeding, and analyzed as to their nature were obtained in 1920 by the author[1] by the use of X rays. When female drosophila were treated with certain doses of X rays it was found that the proportion of exceptional sons and daughters, arising by nondisjunction of the X-chromosomes in the eggs, was greatly increased. The exceptional daughters showed that their genetic formula was XXY by, themselves, producing exceptional daughters and sons. Thus the chromosomal mutation, induced by the X rays, was proved to be passed from parent to offspring and the mechanism of its transfer explained.

Several years later evidence of the production of gene mutations by X-ray treatment was obtained by other investigators.[2] At the time of writing it may be said that all of the different types of changes in the germ plasm enumerated in the previous section have been obtained by X-ray treatment of the germ cells.

The mutations produced by X rays appear to be identical with the same mutations when they occur naturally. There is no reason to believe that any mutations have been obtained as a result of X-ray treatment which do not occur naturally. The effect of the X-ray treatment is, therefore, not to produce a specific kind of mutation but rather to speed up the process in general. X-ray treatment does not, therefore, seem likely to provide a method of producing favorable rather than unfavorable mutations, although a few useful mutations have resulted from X-ray treatment.

The artificial production of heritable changes in the germ plasm by X rays or other physical or chemical agencies should not be confused with the inheritance of acquired characters. In the case of X-ray treatment the germ cells are directly exposed to the treatment and there is no reason to assume that soma cells are involved.

8. HEREDITY AND AGRICULTURE

It must be admitted that most of the important and common varieties of plants and animals used in agriculture were established long before the modern science of heredity, as outlined in this chapter, came into existence. The early agriculturists and to a very large extent farmers all over the world today endeavor to improve their stock and their yield in two ways. (1) By improving the soil, by irrigation, and, in the case of animals, by giving them better food and providing better living conditions — in a word, by improving the environment. (2) By improving the stock, be it plants or animals, by selecting for breeding only the best individuals. It has long been recognized that improvements in the environment, while increasing to some extent the yield, are limited in their effect and that for continuous improvement or even for the maintenance of the yield, it is necessary to use selected stock for breeding. The method of selection has been applied to the breeding of livestock from the earliest times and has led in more recent times to the recording of pedigrees such as those of famous breeds of cattle and race horses. The results of selective breeding provide an irrefutable argument for the potent influence of heredity.

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[1] Mavor, James W., "On the Elimination of the X-chromosome from the Egg of *Drosophila melanogaster* by X rays," *Science*, N.S. Vol. LIV, p. 277, 1921; "On the Production of Nondisjunction by X rays," *Science*, Vol. LV, p. 295, 1922; and "The Production of Nondisjunction by X rays," *The Journal of Experimental Zoology*, Vol. 39, No. 2, April, 1924.

[2] Muller, H. J., " Artificial Transmutation of the Gene," *Science*, July 22, 1927.

The modern science of heredity, with its insistence on the genetic analysis of individuals, has led to the development of more precise and efficient methods for the improvement of stocks. One or two examples must suffice. The importance of wheat as a food has already been stressed. There are a number of characteristics which a good variety of wheat should possess. One of the first to apply genetic principles to this problem was Biffin in England. He found that in a number of cases the desirable characteristics behaved as unit characters and in their inheritance obeyed Mendel's laws. By crossing different varieties he was able to produce a variety having the good qualities of a number of different varieties. Thus into his new variety he introduced the high yield of an English variety, the good bread-baking quality of the Red Fife variety, the resistance to yellow rust of the American Club, the resistance to mildew of Black Persian, and early ripening from a Chinese variety. Since Biffin's work similar results have been obtained with other cereals.

In the case of chickens an important feature is egg laying. A good layer begins early, lays steadily, and continues late, and is seldom broody. These elements have been found to be inherited as unit characters. It is therefore possible to combine in one breed the good qualities of different breeds. This has been done at the Massachusetts Experiment Station. The same sort of experimental breeding is being carried out on cattle with regard to the production of milk.

9. HEREDITY IN MAN

A. IDENTICAL TWINS

Human beings vary greatly in all their characteristics. The shape and structure of the body, physiological and mental activities differ to such an extent that no two persons are alike. The greatest resemblance between individuals is found in the case of so-called identical twins. Such ndividuals arise from a single fertilized egg which accidentally became divided into two parts at an early stage, perhaps as early as the two-celled stage. Since identical twins come from a single egg, each twin has the same set of genes and all of them are in the condition to produce the same characteristics. Identical twins are always of the same sex.

Identical twins, which have been separated early in life and reared apart, offer an opportunity to determine which characters are due to heredity and which to environment. A number of pairs of identical twins have been carefully studied. Such studies show that the individuals remain very much alike even when they have grown up in quite different environments. In other words, in so far as the determination of the physical characters by which the individuals are recognized are concerned, heredity has more effect than environment. Intelligence tests have been carried out on a case of identical twins who were separated at the age of eight months and had been together an aggregate of ten months up to the time of testing. One was trained in a business college and has held numerous secretarial positions; the other has been a teacher, s married, and has one child. The intelligence tests show remarkably close ratings. However, tests calculated to determine will power, emotion, social qualities, and the like show considerable differences, indicating that these qualities were affected by the differences in training and environment. Other tests of twins who appeared to be physically identical have not shown the same identity in mental tests. Definite conclusions regarding the effects of environment and training on the mentality of dentical twins must await further data and studies. However, it can be said that individuals who are so much alike in early childhood as to be abeled "identical twins" remain alike throughout life even when they ive in different environments, which shows that the characters by which we differentiate people are determined mainly by heredity.

B. MENDELIAN CHARACTERS IN MAN

Our knowledge of Mendelian or other possible hereditary characters n man is, for obvious reasons, based almost entirely on a study of pedigrees or genealogical trees. It is often, one might say usually, difficult to obtain the accurate information required to construct such trees. Usually only very striking or peculiar characteristics can be traced through a number of generations. Hence a list of the known Mendelian characters n man contains a large number of pronounced abnormalities or peculiar characters. There is no reason, however, to conclude that only such characters, or mainly such characters, are inherited. Indeed there is reason to believe that the vast majority of characters and traits which are associated with family likeness are inherited and that their inheritance conforms to Mendel's laws.

In attempting to appraise our present knowledge of human heredity, consideration must be given to the difficulites and handicaps geneticists are under in studying inheritance in man. It is only very rarely that the investigator has an opportunity to observe more than three generations and he is fortunate if he is able to observe two generations. Beyond this he must depend largely upon tradition, since personal characters are seldom made a matter of written record. Many characters about which we would like information are difficult to describe. The making of comprehensive genealogical trees, the only method by which the inheritance of human traits can be studied, is therefore attended with great difficulty. Many inherited characters depend on environmental conditions for their expression; for example, susceptibility to a disease can be determined only by exposure to the disease, a particular kind of ability can be demonstrated only when there has been an opportunity for its exercise. Certain characters appear only in the adult or later life and so can be determined only for those children who live to that age. Many traits may appear in so inconspicuous a form that they pass unobserved. Similar traits may be due to different hereditary factors. Many traits are undoubtedly due to the interaction of a number of genes. The investigator has no opportunity to test his conclusions by experimental breeding as is done in the case of animals, but must simply search for more data for comparison with that already obtained.

Only in special cases can information of much value be given regarding the desirability or undesirability of any particular human mating. Few families have either accurate or extensive genealogical trees and even when such are on record there is always a tendency to ignore "the skeleton in the closet." Certain general considerations may, however, be discussed.

Consanguineous marriages are marriages between persons of near kin. There is a general belief that such marriages are inadvisable and such unions have been the basis of taboos among many primitive and civilized races. The biological principle involved is quite clear. If there is an hereditary defect in the family, particularly one which behaves as a recessive character, there is a considerable chance that both partners, although not showing the trait, may be heterozygous for it and therefore that one fourth of their children, being homozygous for the trait, will show the defect. The principle applies equally well to valuable traits since if the parents are related they are more likely to both have the trait and to pass it on to their children. Thus the important question is not whether the parents are blood relations but whether the genealogical tree shows any recessive hereditary defects. Many famous men and women have been the offspring of consanguineous marriages.

There seems little doubt that mental traits are inherited according to the principles outlined for purely physical traits. Nevertheless, it is difficult to give examples. The diagnosis and description of mental traits is attended with great difficulty. In addition, what we are apt to regard as simple mental traits are in reality often due to the interaction of a number of different traits. Many genealogical trees point to the inheritance of general mental ability, musical ability, artistic ability, and literary ability; but the exact mode of inheritance of these abilities is far from clear. A noted authority states: "In no other groups of diseases is heredity so conspicuous among causes as it is in the case of mental disorders, but at the same time there is no other field in which the study of heredity is so difficult. For, to begin with, specialists are far from being agreed as yet upon the classification and delimitation of the hereditary diseases of the mind. We need hardly be surprised, therefore, that in scarcely one of these diseases has the hereditary cause been satisfactorily established. Only this much is certain, that heredity is the outstanding cause of mental disorders."

10. HEREDITY AND SOCIETY

Among the individuals of a wild species there is constant competition for food and shelter. A multitude of enemies, seen and unseen, contest with each its existence. The result of this is that only the fittest survive and pass on their hereditary characters. One of the chief objects of civilization is to abolish or limit individual competition by cooperative effort and to rout seen or unseen enemies by the collective power and knowledge of the group. The aim of democracy is to give to each individual equal opportunity for the exercise of all human functions, including that of marriage and reproduction. This has led to a condition in which not only do the unfit propagate their kind, but the less fit and shiftless have larger families than the more provident and able portions of the populations. For example "families which send a child to the state home for feebleminded in California were found to average at least half again as large as those that send a child to the state university."

The success of experimental breeding in developing useful varieties of animals and plants has suggested to social philosophers its application to the human race. There are, however, certain important differences between the problem of the agriculturist and that of society. First, the breeder has in mind certain definite characters which he wishes his animals or plants to possess, such as beef production, egg production, speed, or crop yield. Who except a nationalist dictator would undertake to prescribe the characters which a member of the human race should possess? Second, the breeder is master of his herd and can make his matings unrestrained by any considerations of ethics, politics, or the happiness of the individuals concerned. Third, the breeder has already or can obtain by experimental breeding a knowledge of exactly how the characters he is concerned with behave in heredity.

Although these conclusions make it evident that the question of the creation of a superior human race must be relegated to the realm of speculation, the social importance of heredity cannot be denied. The following facts have been amply demonstrated: First, what any individual becomes depends partly on his environment and partly on his heredity. Second, many undesirable and also many desirable human traits are inherited and in a few cases the mode of inheritance is known.

An example of the effect of the environment on a social group is given below. In Norway careful records are kept of the height and weight of school children. The table (Table 38:3) is compiled from measurements made in 1920 and 1930 in the same schools and of children of the same ages. When the heights and weights of children of the same age and sex are compared the difference is striking; for example the average weight of a fourteen-year-old boy in 1930 was 4.1 kilograms (approximately 8 pounds) more than that of the average boy of the same age in 1920. As it is very unlikely that there was any change in the hereditary characteristics of the children sent to the schools in the different years it seems clear that the increased height and weight must have been due to improvements in the environment, including nutrition, which are known to

TABLE 38:3. THE AVERAGE HEIGHT AND WEIGHT OF SCHOOL CHILDREN IN NORWEGIAN SCHOOLS IN 1920 AND 1930[1]

AGE	SEX	HEIGHT IN CM		INCREASE	WEIGHT IN KG		INCREASE
		1920	*1930*		*1920*	*1930*	
10	Boys	130.9	135.1	4.2	27.6	29.9	2.3
	Girls	130.0	134.6	4.6	27.0	29.8	2.8
14	Boys	148.2	153.1	4.9	38.5	42.6	4.1
	Girls	150.6	154.9	4.3	41.8	45.5	4.3
18	Boys	173.6	176.1	2.5	62.3	64.3	2.0
	Girls	161.6	164.7	3.1	52.9	56.9	4.0

[1] Simplified from Otto L. Mohr, *Heredity and Disease*, W. W. Norton & Company, Inc., New York, 1934.

have occurred during that time. The responsibility of society in this regard is, therefore, clear. Once a child is born every effort should be made to provide for it a suitable environment.

With regard to heredity the problem is more difficult. Undesirable and desirable characteristics occur in the same individual — Napoleon and Caesar were epileptics — and no method is available to separate the desirable characters from the undesirable as can be done in animal and plant breeding. Certain characters, however, so handicap the individual that they would seem to outweigh any good characters which he might possess. An example is feeble-mindedness. There are various grades of feeble-mindedness and not all types are inherited. Studies of the inheritance of feeble-mindedness have shown that in a few cases feeble-mindedness behaves as a Mendelian recessive. The number of feeble-minded in the United States is variously estimated at from three hundred thousand to five hundred thousand. Only a small percentage of these, perhaps 10 per cent, are in the care of the various states. One obvious remedial measure is to prevent the reproduction of the feeble-minded. This can be and is to some extent done in the case of those in state institutions. But even if it were possible to prevent the reproduction of every feeble-minded individual, the problem would be far from solved. Feeble-mindedness being a recessive character can be carried in the heterozygous condition by a normal person and in this condition may pass through a number of generations if the heterozygous carriers always marry normal individuals. The same difficulty presents itself in all attempts to eradicate undesirable recessive characters from the human race.

The problem is simpler in the case of dominant characters. In this case the character appears in the heterozygous as well as in the homozygous individuals. Therefore the character can be transmitted only by those individuals who show the character and if they have no children the character will die out.

The improvement of the human race by increasing the number of gifted and physically fit individuals is another important aspect of the problem. It seems unlikely that this will become, at least in the near future, the subject of collective action. Responsibility rests with the individual who possesses the desirable characters: they are in his trust. It is the duty of every man and woman who contemplates marriage to obtain all the information possible regarding the heredity of each and to act accordingly. This they should do not only in the interest of the future generation but for their own happiness.

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Questions

1. Why is heredity concerned mainly with the offspring of sexual reproduction?
2. Classify variations.
3. Discuss, using examples, the relation between heredity and environment.
4. Are acquired characters inherited?
5. Explain the relation between a gene and a bodily characteristic.
6. Describe and explain the results of a simple cross between a black and a white guinea pig.
7. Backcross the F_1 of the above example and explain the result.
8. Define heterozygous, homozygous, recessive, dominant, partial dominance, genotype, phenotype, backcross, free assortment.

9. In the garden pea yellow seed-color is dominant to green seed-color and smooth seed coat to wrinkled seed coat. Cross a yellow, wrinkled-seeded plant to a green, smooth-seeded plant. Describe the F_1 and the F_2 obtained by inbreeding the F_1, as regards phenotypes and genotypes.
10. Describe and explain the results of crossing a short-haired black guinea pig with a long-haired white guinea pig. Inbreed the F_1 and describe the F_2 phenotypically and genotypically. Short hair is dominant.
11. State the four principles of Mendelian inheritance and show by examples how the inheritance of genes conforms to them.
12. Explain how linkage and crossing over occur.
13. The gene which determines whether the wings will be "miniature" or "long" in *Drosophila* is located in the X-chromosome. "Long" is dominant over "miniature." Describe and explain the result of crossing a "miniature" female with a "long" male. Inbreed the F_1 and describe the F_2.
14. Red-green color blindness is a sex-linked recessive character in man. What are the chances that the son of a color-blind man and a normal woman will be color-blind? That the son of a color-blind woman and a normal man will be color-blind? Consider the different possibilities involved.
15. Classify the kinds of changes (mutations) which are known to occur in the germ plasm.
16. How have mutations been artificially produced? Distinguish between this and the inheritance of acquired characters.
17. What light has been thrown on heredity by the study of identical twins?
18. Discuss consanguineous marriages.
19. What can be said of the inheritance of mental traits?

Suggestions for Further Reading

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PART VI. The Organic World and Its Evolution

CHAPTER 39

Animals and Plants in Relation to Their Environment

In the previous chapters, we have looked at organisms chiefly as individuals taken out of their natural relations to the physical world around them and to the other living creatures which affect their lives. Yet what an organism is and whether it continues to exist depends quite as much on its environment as on its structure and physiology. This environment consists not only of that part of the inanimate world with which the plant or animal comes in contact, and of the physical and chemical changes to which it must respond, but also of a part of the animate world, which consists of those other plants or animals which in any way affect its existence. The study of the relations of plants and animals to their environments, animate and inanimate, is called **ecology,** from the Greek, *oikos,* a house or dwelling.

1. THE ENVIRONMENT

A. THE INORGANIC ENVIRONMENT

The chemical substances and the various physical agents which constitute the inorganic or nonliving elements of the theater in which the drama of life goes forward vary much from place to place on the surface of the earth.

(1) THE CHEMICAL ENVIRONMENT

(a) WATER

It is scarcely necessary to emphasize the fact that water is essential for life and is therefore a necessary constituent of the environment of all organisms. For aquatic plants and animals, whether marine or fresh water, it is the medium in which they live. For land plants or animals it must be available in the soil and present in the air. Indeed, the distribution of living things corresponds fairly closely to the distribution of water over the surface of the globe, and on land they are in general most abundant where the humidity is greatest.

No other substance is known which could play the part which water plays in living processes. Some of the unique characteristics of water which make it particularly fitted to play this role are its solvent power, its ability to ionize substances in solution in it, its chemical inertness, and its high surface tension.

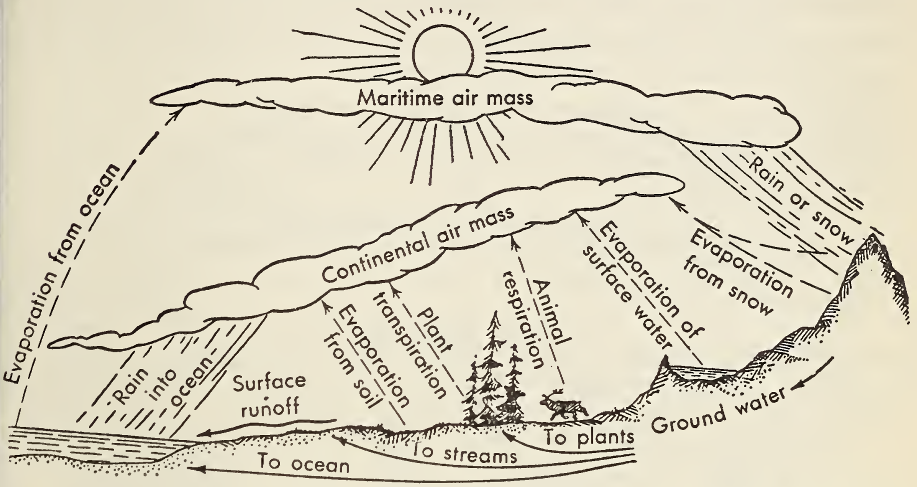

Fig. 39:1 The water cycle. The interchange of water between the atmosphere, land, and sea is a major factor in producing the soil so necessary to most land plants and the seasonal changes which affect all organisms. Water is evaporated from the ocean and carried over the land where it becomes precipitated as rain or snow. Water is also evaporated from the soil and from the bodies of plants and animals to be later precipitated over the land or sea. From T. I. Storer, *General Zoology*, McGraw-Hill Book Company, Inc.

There is some doubt as to whether life began in the sea or in fresh water but there is practically general agreement that it must have arisen in water somewhere. Today the greatest variety of forms is found in the ocean and all the more primitive forms of plants and animals are found either in the ocean or in fresh water.

"As a solvent there is literally nothing to compare with water. . . . In the first place the solubility in water of acids, bases, and salts, the most familiar classes of inorganic substances, is almost universal."[1]

Water, due to its physical properties, goes through a **cycle** (Fig. 39:1). It is constantly being evaporated from the surface of the earth into the atmosphere to be precipitated as rain and flow over and through the soil. This movement of water and its unequaled solvent power is one of the main factors in the disintegration of rocks and the cause of the salinity of the ocean.

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[1] Henderson, L. J., *The Fitness of the Environment*, The Macmillan Company, New York, 1913, p. 111.

(b) CARBON DIOXIDE

Although carbon dioxide is present in the atmosphere in very small quantity (0.03 per cent) it is essential for green plants and thus for the existence of all higher life on the earth. Carbon dioxide and water provide the raw materials for photosynthesis. The presence of carbon dioxide "in the atmosphere insures the occurrence of greater, or at least equal, quantities in the ocean and in all the natural waters of the earth."[1] This is due to the solubility of carbon dioxide in water. It is such that under ordinary conditions the quantity of carbon dioxide in a given volume of water is approximately equal to the quantity in an equal volume of air. Thus it is equally available for green plants in the water of the soil, rivers, lakes, and the ocean. Carbon dioxide enters and leaves water freely. It, therefore, everywhere accompanies water and circulates with it. Carbon dioxide is the chief food of plants and it possesses two

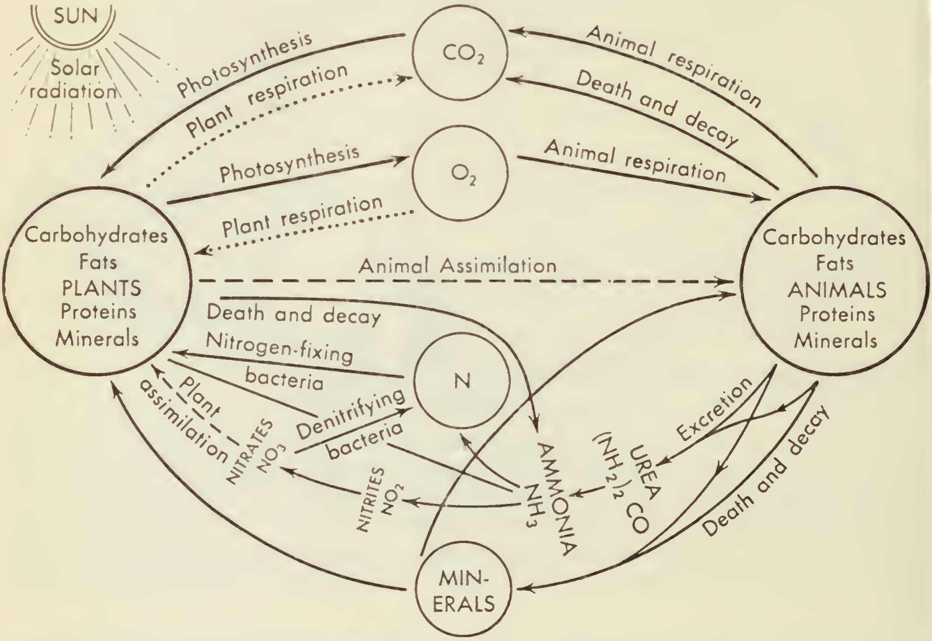

Fig. 39:2 The chemical cycle. Most of the chemical elements entering into the metabolism of animals and plants pass through a cycle in which they are at one time in organisms and at another time in the inorganic world. From T. I. Storer, *General Zoology*, McGraw-Hill Book Company, Inc.

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[1] Henderson, L. J., *op. cit.*

very important qualifications for a food; it occurs everywhere and it is constantly being moved from place to place so as to be available everywhere.

Carbon dioxide is practically the only form in which the element carbon passes from the inorganic to the organic world and it is chiefly in this form that it returns from the organic to the inorganic world. Taken in by green plants, it is combined with water in the photosynthetic process to form sugar, and it is from this sugar that the carbon contained in the carbohydrates, fats, and proteins of plants and animals is obtained. Carbon passes through a **cycle** during one part of which it is in the atmosphere as carbon dioxide and the other part of which it is a constituent of organic matter (Fig. 39:2). Fresh water, made slightly acid by the presence of carbon dioxide from the air, dissolves sodium, potassium, calcium, and magnesium from the soil to form bicarbonates. These salts of carbonic acid when present with the acid serve to maintain a system of buffers in natural waters. Carbonic acid is one of the few acids which possess in a high degree the capacity to form buffer solutions with its salts. "All acids whose strength is even a little either greater or less than carbonic acid lack this property."[1]

(c) OXYGEN

We are inclined to consider oxygen the most important constituent of the atmosphere, chiefly, perhaps, on account of our own requirements of that element. Yet the role which oxygen plays in living processes apart from being a constituent of most of the compounds concerned is that of aider and abettor of destruction. Oxidations are usually involved in the breaking down of organic substances although the energy thus released may be used by the organism to build up other substances.

Oxygen in its uncombined form is not essential to all organisms. Some plants and some animals can utilize combined oxygen to carry out the oxidations which their living processes require. Such organisms are said to have anaerobic respiration in contrast to the aerobic respiration of other organisms. They include many kinds of bacteria, yeast under certain conditions, some annelid worms, and a number of animal parasites.

(d) NITROGEN

The nitrogen **cycle** has already been referred to in the chapter on bacteria. By far the greater part of the nitrogen either on or near the surface of the earth is in the atmosphere, of which it forms approximately

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[1] Henderson, L. J., *op. cit.*

79 per cent. The remainder is largely in the form of compounds which have been formed in the bodies of plants or animals or the decomposition products of these.

Most land plants obtain the nitrogen they require from the nitrates in the soil. These nitrates are there largely as the result of the action of nitrifying bacteria acting on decay products and nitrogen-fixing bacteria which take nitrogen from the air. The nitrates from the soil are carried in the soil water to streams and ponds and thus become available to all fresh-water life. Some of these nitrates are carried in the water of rivers into the ocean.

(e) OTHER ELEMENTS

The other elements required by plants and animals come into the soil and the soil water as products of the disintegration of rocks and erosion of the soil (Fig. 39:3). This disintegration and the distribution of the resulting inorganic salts is brought about largely through the water cycle (see Sec. (1)).

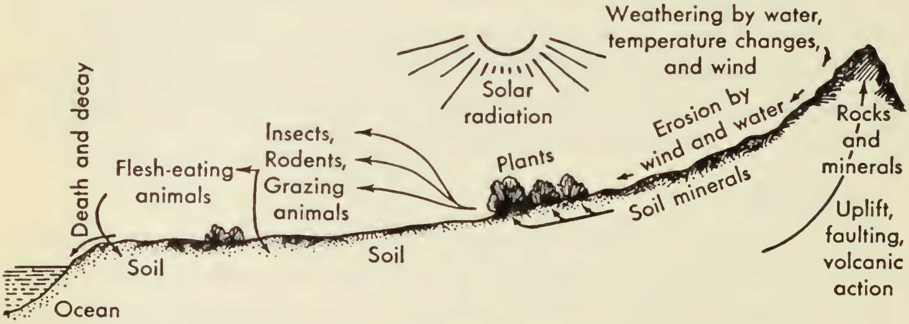
Weathering by water, temperature changes, and wind
Solar radiation
Death and decay
Insects, Rodents, Grazing animals
Flesh-eating animals
Plants
Erosion by wind and water
Rocks and minerals
Soil minerals
Uplift, faulting, volcanic action
Soil
Soil
Ocean

Fig. 39:3 The mineral cycle. Rocks become disintegrated into soil. The soil becomes eroded and is transported by water toward the low lands. The soluble materials become dissolved in the soil water and are eventually carried into rivers and lakes and to the sea. From T. I. Storer, *General Zoology*, McGraw-Hill Book Company, Inc.

(2) PHYSICAL AGENTS IN THE ENVIRONMENT

(a) LIGHT

Primitive man and the men of the early civilizations recognized the importance of light for life in their almost universal worship of the sun. Life, as we have already seen, is essentially a question of energy changes. Energy is taken from the environment and appears in the varied activities of the organism. The prime source of energy for all life is radiant energy from the sun. Only green plants have the power to capture and transform this energy. Hence all organisms with the exception of the small group of autophytic bacteria are ultimately dependent upon green plants and through them upon the sun.

The amount of light and heat (radiant energy) received by the earth from the sun is enormous. At any given place it depends upon the time of day, season of the year, latitude, and the condition of the atmosphere. During a clear day in summer at latitude 45° a square yard on the surface of the earth receives in the form of radiation from the sun somewhere between 2000 and 5000 kilogram calories, or about enough energy, if it could be transformed without loss into absorbable food materials, to support one man. However, only a small fraction of this energy is used in photosynthesis,[1] the greater part going to raise the temperature of the surroundings. With the most efficient agriculture and fertile land about 1 acre, 4840 square yards, is required to raise enough food for one man.[2]

Light acts as a direct stimulus for many of the activities of plants and animals and in this capacity is of great importance. Examples have already been discussed and more will appear in later sections.

(b) *TEMPERATURE*

Except in special cases active life occurs only between 0°C (32°F) and 45°C (113°F). Many sea fishes and other animals remain active and many marine algae continue to grow at temperatures one or even two degrees below zero Centigrade since the salinity of the sea water prevents it from freezing at these temperatures. Certain invertebrates are known which live in hot springs where the temperature may reach 50°C (122°F) or more and algae have been found growing in water at temperatures up to 80°C (176°F). The dry spores of certain bacteria can withstand temperatures of 120–130°C (248–266°F).

For most organisms there is a **minimum temperature** below which they cannot carry on their vital processes, a **maximum temperature** above which they become inactive and eventually may die, and an **optimum range of temperature** within which they thrive best. Thus tropical plants and animals do best at temperatures above 32.2°C (90°F) and are easily killed by cold weather, while temperate plants thrive best at temperatures between 15.5°C (60°F) and 32.2°C (90°F). Arctic plants grow at temperatures only a little above freezing.

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[1] See Chap. 16, Sec. 5, for a discussion of the efficiency of the photosynthetic process.

[2] The calculation is as follows: the average man needs 3000 calories per day or 1,095,000 calories per year. One pound of wheat yields approximately 1600 calories. One bushel of number one wheat weighs 58 pounds and yields approximately 92,800 calories. Therefore if a man could live on wheat alone (as many Chinese do on rice, which is very similar to wheat), he would require 1,095,000/92,800 = 11.8 bushels per year. The average yield of wheat per acre in the United States was, in 1934, 11.8 bushels per acre. The calories used in this calculation are kilocalories.

Many organisms require a seasonal change of temperature. Thus the seeds of many temperate plants will not develop unless subjected for a period of time to temperatures below freezing and the same is true of the eggs of many insects. The cold of winter has become a necessity to them.

(c) CLIMATE

The term **climate** has been used to include the condition which results from a combination of physical factors, the chief of which are temperature, sunlight, and water vapor. In general, when traveling from either pole to the equator each of these factors increases in intensity. There may, however, be geographical factors which change this succession. Thus in going up a mountain, even at the equator the temperature decreases so that at great heights it may approach that of the arctic regions. Also in going from east to west across the southern United States all stages of humidity are encountered from relatively humid forest regions to dry deserts.

B. THE ORGANIC ENVIRONMENT

The organic environment consists of the other organisms which in any way influence the life of the individual under consideration. In some cases the relation brings **mutual benefit.** Thus in the pollination of higher plants by insects both the insect and the plant benefit, the plant by the transfer of its pollen, the insect from the nectar or pollen which it uses as food. Somewhat the same relationships exist in the case of seed dispersed by birds and mammals. The birds or mammals eat the fruit and disperse the seeds. Organisms of decay, including bacteria and other fungi, serve the entire organic world by making available again the materials needed by protoplasm. The autophytic bacteria also aid the growth of green plants by bringing nitrogen into the soil. The benefit may be somewhat one-sided as in the case of the many animals and plants which find shelter in a forest, shrubbery, or grassland.

Plants or animals may derive mutual benefit from association. Thus the trees in a forest are better able to weather storms by being together rather than isolated; grasses by being in clumps hold more moisture and organic material in the soil than when separated. Grazing animals commonly go in herds where they find protection from their carnivorous enemies. Many animals associate in groups for breeding purposes, building their nests together or swimming in shoals. Climaxing this type of association are the social insects already described in a special chapter (Chap. 24).

The relationship may be one of **competition.** Plants compete for soil, water, and light; animals for food. The competition may be between individuals of the same species or between different species. The number of individuals of a species in a given locality is frequently determined by the amount of food available. "Food chains" for a number of different types of plant-animal communities have been worked out. Examples are outlined in the diagrams (Figs. 39:16 and 39:34). Here the relative number of individuals of each species is to a certain extent dependent on the relative number of individuals of the species which feed upon it and the species which it feeds upon.

Not only is each species adapted in its own way to the particular conditions of its particular environment, but the different species of plants and animals inhabiting any region are intimately associated and form a community. A number of **plant-animal communities** are described in the sections which follow. The kinds of plants and animals which live in a community are determined in the first place by the chemical and physical conditions of the region and the seasonal changes of these. Depending on such conditions certain species which are well adapted to them are abundant. These species are said to be the dominant species and give the community its general characteristics. Thus in a forest community one or more species of trees are dominant; the forest may be a pine forest, a maple forest, or it may be a maple-beech forest with some oak as in the community described in Sec. 2, A. Again, the community may be on the seashore and be that of a mussel shoal where mussels are the determinant species, of an oyster bed where oysters are dominant. Just as the cells, tissues, and organs of an individual plant or animal are organized to form its body and carry on its vital activities so the different species of plants and animals are brought together by the special conditions of their environments and their modes of life to form communities in which each has its place or niche.

2. LIFE ON LAND[1]

The North American continent is largely a continent of forests and prairies with lesser areas of shrubby woodland and desert. Perhaps it is better to say that it was such a continent, for since the white man came with his axe and plow much of the forest and most of the prairie have been made into farm land. Stretching across the northern part of the continent and extending southward along the mountain ranges of the East and West is a great **coniferous** or evergreen forest, i.e., one composed largely of trees which bear cones and carry their leaves through the winter. This is where most of our lumber comes from — where the Douglas fir, the black and white spruce, giant cedar, balsam fir, and lodgepole pine dominate the landscape. Most of the eastern half of the

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[1] For the classification of the various plants and animals referred to in this chapter the student should consult the Appendix.

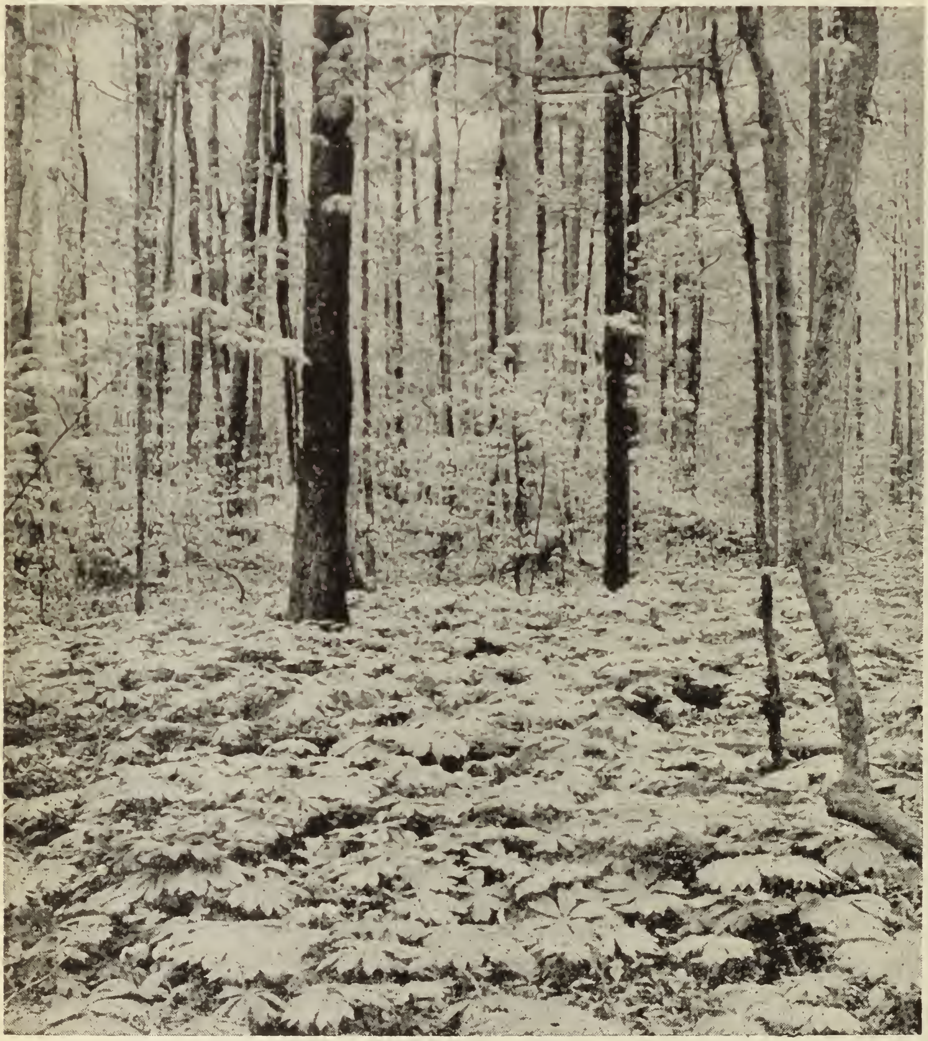


Fig. 39:4 Typical forest ground cover in the spring, mayapple (*Podophyllum*, class Dicotyledoneae, order Ranales, family Berberidaceae). Photograph by L. W. Brownell.

United States extending from the Mississippi Valley to the Atlantic seaboard was occupied by a temperate **deciduous** forest, i.e., one in which the leaves of the trees fall in the winter. West of this eastern temperate forest and extending over the great plains to the Rocky Mountains were the great prairies or grasslands. West of this again are the vast forests of the Rocky Mountains.

A. LIFE IN A FOREST

A temperate deciduous forest is chosen for description. Such a type of forest varies somewhat in different parts of the East. In the following description only a few of the common and more generally distributed plants and animals are considered so that the discussion may be applied to almost any deciduous forest in the eastern United States and with slight modifications to any temperate forest. A common type of broad-leaved forest is that in which beech, maple, and oak are the most abundant trees although other broad-leaved trees such as hickory, chestnut, poplar, and birch and some conifers such as the pine and hemlock may be abundant. These trees will grow only where the climate, soil, and other environmental conditions are suitable. There must be a moderate rainfall, 25 to 60 inches per year. The summer must be moderately warm with an average temperature between 60° and 65°F and they seem to thrive best when the winter temperature goes below freezing. The falling of the leaves in the deciduous forest is an adaptation to the contrasting conditions of summer and winter. The broad leaves enable the trees to manufacture starch and carry on their vital activities at a maximum rate during the summer when there are long periods of sunlight, a warm temperature, and usually plenty of moisture. On the other hand, in the winter when the days are short and cold and the air dry such leaves would be a definite disadvantage to the plant through loss of water from their surfaces. So the leaves are shed and the plant becomes dormant. The trees are said to be the dominant plants in the forest because they determine to a large extent what other forms of life can exist there.

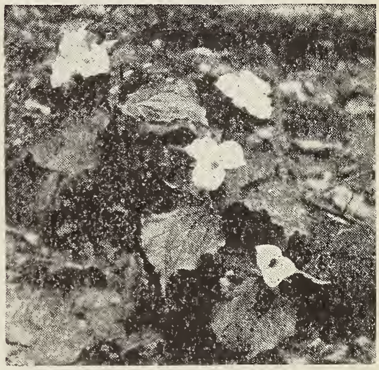


Fig. 39:5 A spring wildflower common in the woods, the white trillium or large-flowered wake-robin (*Trillium*, class Monocotyledoneae, order Liliales, family Liliaceae). Photograph by Arthur B. Williams, Cleveland Museum of Natural History.

Like all green plants, trees compete for sunlight. They are able to overshadow their competitors because they can grow high and spread their leaves.

Many of the conditions within the forest are determined by the trees. In summer the leaves cast a deep shade, tremendously reducing the intensity of the sunlight and making it impossible for plants requiring much light to grow beneath them. These same leaves which shut out the sun keep the air inside the forest moist during the summer so that it is saturated or nearly saturated. Trees also provide protection from wind and rainstorms. Their dead leaves and fallen trunks are the source of a large part of the organic matter in the soil. Thus the trees are not only the largest organisms of the forest but they are also responsible in large measure for the existence of the community which they dominate.

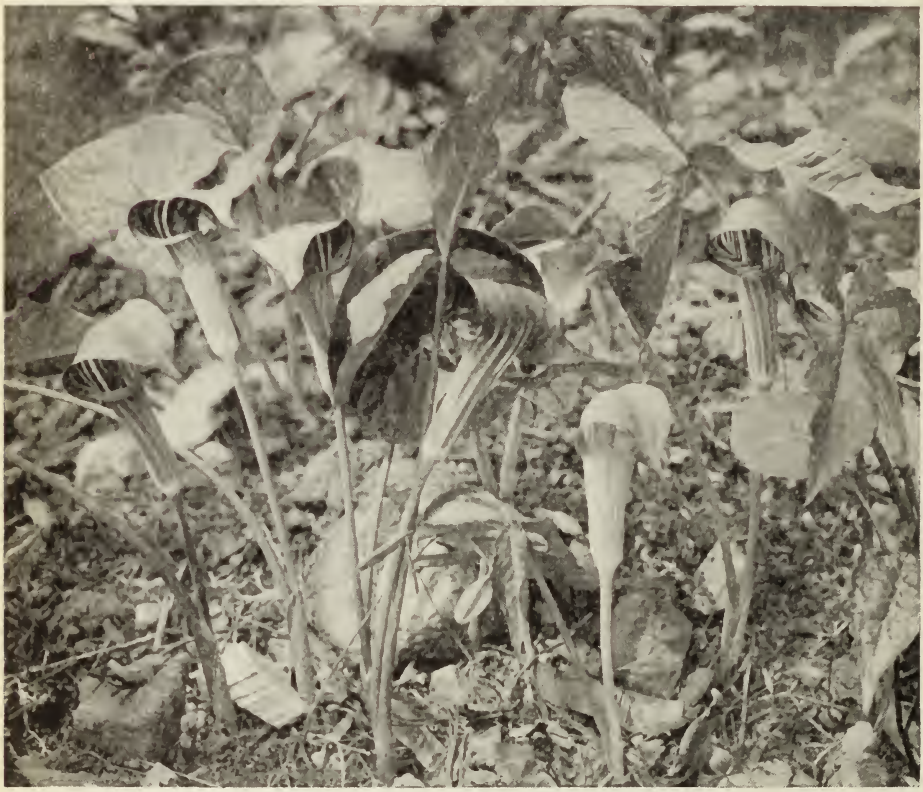


Fig. 39:6 Jack-in-the-pulpit (*Arisaema*, class Dicotyledoneae, order Arales, family Araceae). Photograph by L. W. Brownell.

Where the trees of the forest are farther apart and more sun gets through, smaller trees and shrubs occur such as mayapple (Fig. 39:4), sassafras, pawpaw, wild cherry and wild grape, all of which produce fruits on which many birds and other animals feed. Trailing over the ground or climbing on the bushes may be bittersweet, its bright scarlet berries adding to the colors of autumn. Close to the ground are many small herbaceous plants with soft stems and leaves. Most of these grow up rapidly in the early spring before the trees get their leaves and while there is still light in the forest. This they are able to do because of nourishment stored underground during the winter in fleshy roots, stems, or leaves. These plants give us most of our spring wild flowers of the forest (Fig. 39:4), such as hepatica, trillium (Fig. 39:5), wild geranium (Fig. 3:8), blood-root, Jack-in-the-pulpit (Fig. 39:6), also known as "Indian turnip" because of its root, violet, and Dutchman's-breeches. The wood nettle is sometimes common. There may be a few ferns (Fig. 3:6) scattered here and there but they are usually not abundant in this type of forest. Mosses are abundant on the fallen trees and stumps.

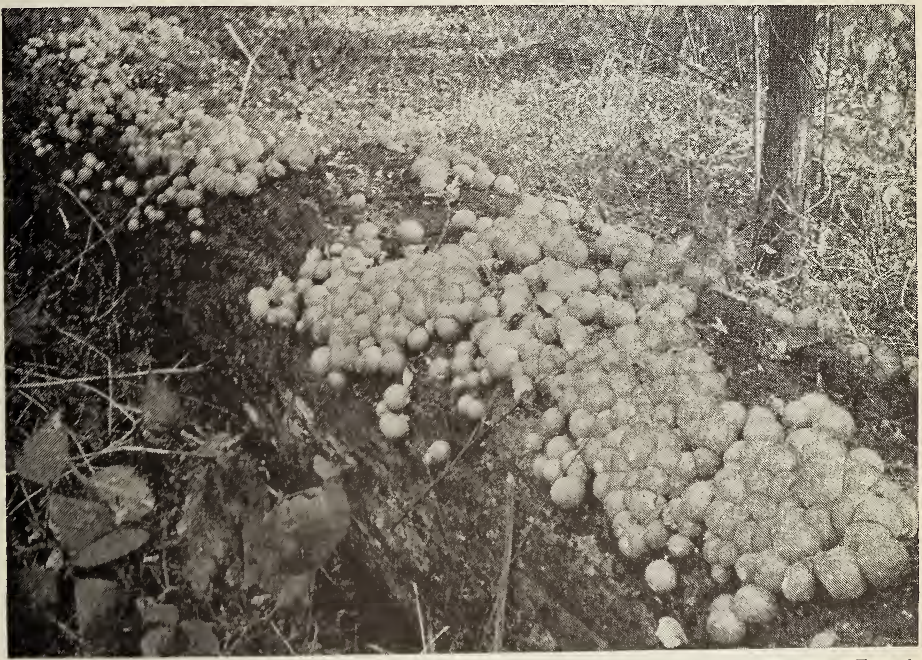


Fig. 39:7 A group of "puff-balls" (*Lycoperdon*, phylum Thallophyta, subphylum Fungi, class Basidiomycetes) on a log. Photograph by L. W. Brownell.

Beneath the green foliage the ground is covered with decaying leaves and twigs which gradually disintegrate to form a brown mealy material called **humus.** The decay which leads to the formation of the humus is brought about by numerous species of fungi (Fig. 39:7), not the least important of which are bacteria. The bacteria are, of course, invisible. The other fungi appear on the surface only when they send up reproductive bodies forming spores. Such are the familiar mushrooms, puffballs, and shelf fungi. These plants do not require light and thrive in the relative darkness of dense vegetation. They are not alone, however, in having found a way to subsist on the abundant decaying material of the forest floor. Among them are a few flowering plants, such as the ghostly white Indian pipe (Fig. 39:8), which entirely lacks chlorophyll.

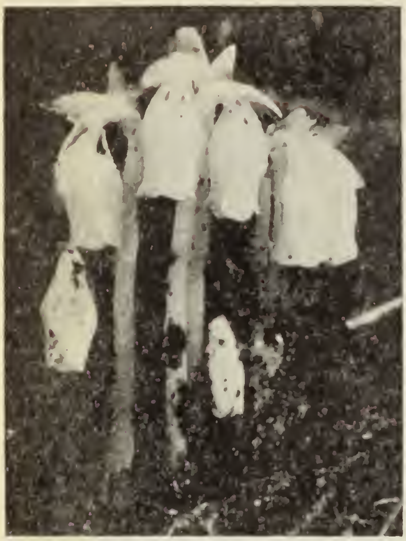


Fig. 39:8 The Indian pipe (*Monotropa*, class Dicotyledoneae, order Ericales, family Ericaceae), a saprophytic flowering plant. Photograph by J. W. Mavor.

For many of the smaller animals one must look among the dead leaves on the forest floor or in tree stumps or under stones. Turn over almost any large flat stone and a miniature world is revealed. Sow bugs (Fig. 39:9) and centipedes (Fig. 3:20) scurry away to cover, beetle larvae squirm, and millipedes curl up and feign death. Perhaps an ant nest has been disturbed and the workers hurry off carrying eggs and larvae.

Insects abound in any forest and each type of forest has its characteristic population of leaf-eating insects, many kinds of beetles, butterflies and moths, bees, wasps, and flies including midges and mosquitoes. Where there are flies, crafty little spiders spin their webs.

Dig under a fallen tree or tear away the rotting wood from an old stump and you may find a salamander (Fig. 3:24). Being amphibians, these little creatures require the humidity of the forest floor. They feed on insects.

If you are lucky you may see a small lizard (Fig. 39:10) basking in the sun near his hiding place into which he will dart should you approach too near. Or you may stir up a snake in the leaves at your feet and hear him scurry away. The smaller lizards and snakes are chiefly insect eaters while the larger snakes feed on shrews, mice, and small birds.

Wild mice, although small, are important animals in the forest on account of their numbers. One of these is the white-footed or deer mouse (Fig. 39:11). The name "deer mouse" was given to it because it was formerly thought to change its coat in a manner similar to that in which the deer changes his. These mice are creamy white underneath and have large ears. Like their domestic brothers they are active chiefly at night.

They live in burrows and underground runways. Under almost any decaying log may be found some sign of their activities — remains of a meal of acorns, a pile of seeds, or the opening to a burrow. The staple foods of the deer mouse are maple seeds, beechnuts, acorns, basswood seeds, and cherry pits but it will eat other things including roots and even moths and flies. By hiding during the day and feeding at night mice escape many carnivorous animals but not the little shrews.

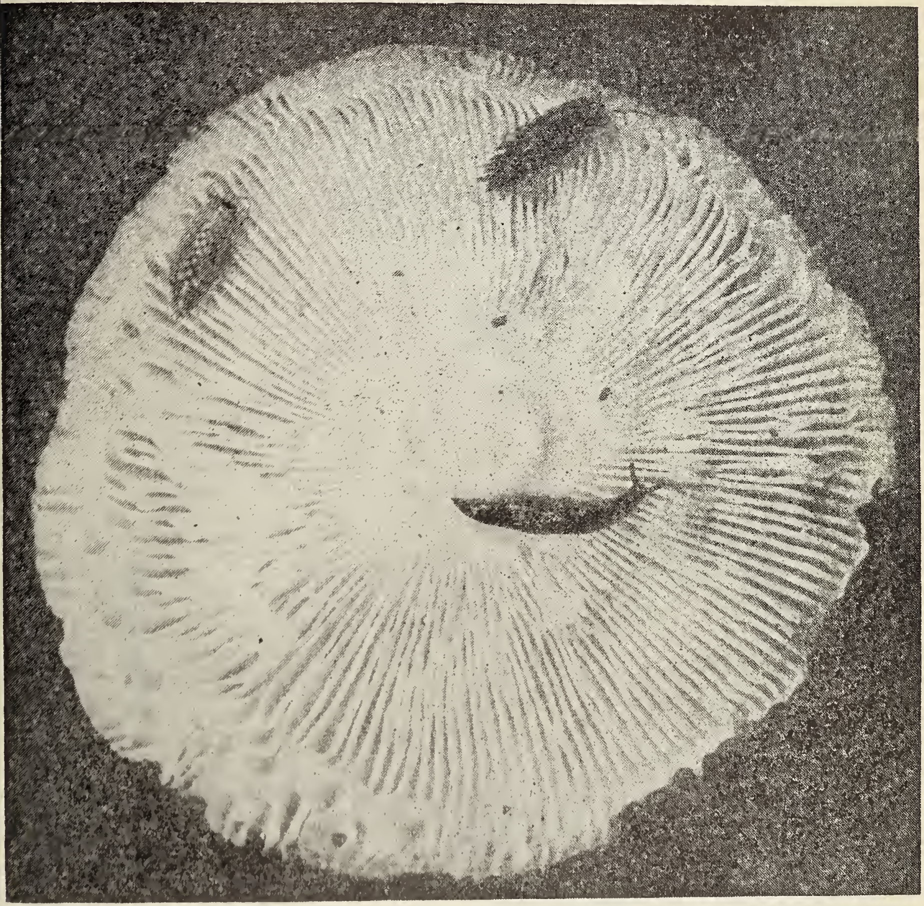


Fig. 39:9 Forest invertebrates on the underside of a mushroom. Above and to the left, sow "bugs" (*Oniscus*, phylum Arthropoda, class Crustacea); near the center, a slug (phylum Mollusca, class Gastropoda). Photograph by J. W. Mavor.

Shrews resemble mice somewhat in size and appearance. Like mice they live in burrows but unlike them they feed chiefly on small animals including mice and insects.

The gray squirrels (Fig. 39:12) commonly seen in parks are but the remnants of vast numbers which inhabited the deciduous forest until the latter part of the last century. In the warm months of the year the gray squirrel builds nests of leaves and twigs in the crotches of trees. The young are born in these nests. The gray squirrel is well adapted to life in the forest. Its short muscular legs and sharp claws enable it to run up and down trunks and branches with the greatest ease. Even its ornamental bushy tail is in reality an adaptation to arboreal life since it serves as a balancing organ when climbing and as a sort of miniature parachute should he accidentally fall. He feeds chiefly on nuts but also eats seeds, leaves, roots, mushrooms, and even birds' eggs. By their habit of burying nuts, squirrels make an important contribution to the life of the forest. Although they return for some of those they hide, numbers are left in the ground to germinate. They are responsible for the planting of many trees, especially hickory.

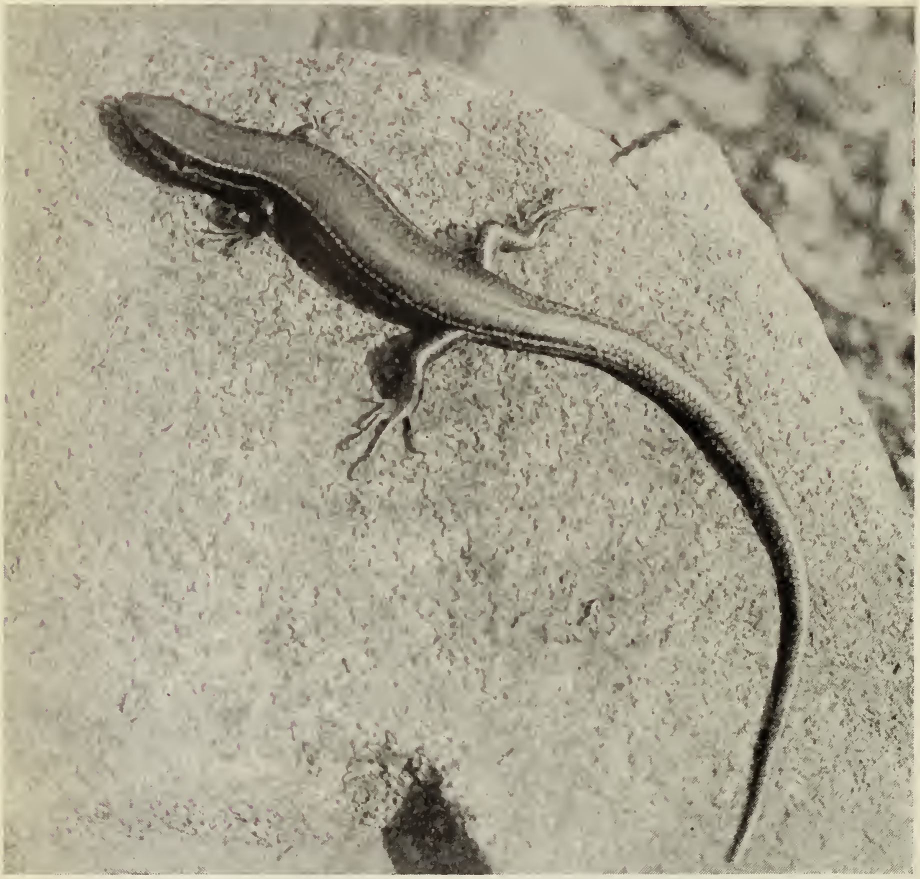
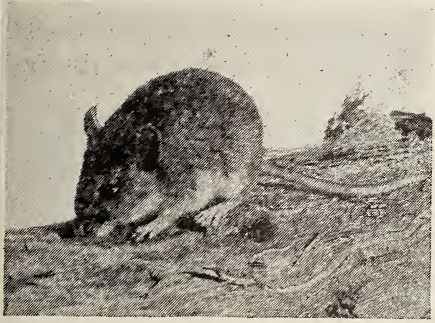


Fig. 39:10 Five-lined or blue-tailed skink (*Eumeces*, class Reptilia, order Squamata, suborder Sauria). Photograph by L. W. Brownell.

The smaller animals of the forest provide food for the larger carnivores. Among these are the foxes of which the commonest and most widely distributed in America is the red fox. This animal resembles a small dog. It is not confined to the forest but may also occur in woodland or open country. Foxes live in dens, a family occupying a den. They hunt singly, i.e., not in packs like wolves, and may go a distance of 5 or 10 miles from the den in search of food. In this they are not very particular, but birds and small mammals are preferred.



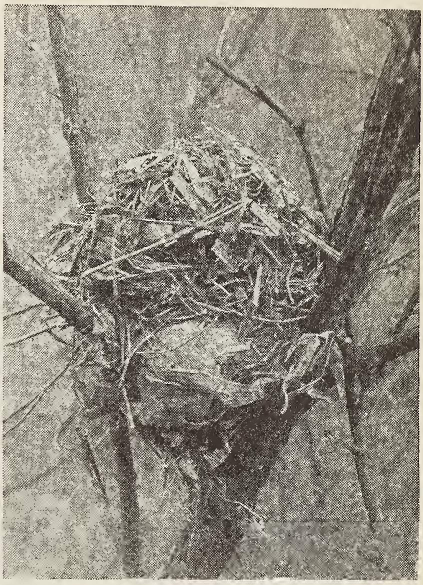


Fig. 39:11 Above, a very common mammal in forests, the white-footed deer mouse (*Peromyscus*, class Mammalia, order Rodentia). Photograph by Arthur Williams, Cleveland Museum of Natural History. At right, nest of a white-footed deer mouse in old nest of a woodthrush. Photograph by L. W. Brownell.

In the early days of the settlement of eastern North America Virginia deer (Fig. 39:13), also known as white-tailed deer, were particularly abundant. The success of the deer as a forest animal, in the absence of man or under his protection, is due partly to its size which ensures it from attack by the smaller carnivorous animals of the forest, its speed which enables it to run from its larger enemies such as the timber wolf, and its ability to exist on a varied vegetable diet including the bark, buds, and leaves of trees, nuts, acorns, grass, and other herbs.

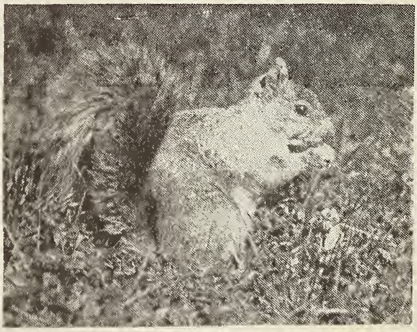


Fig. 39:12 Gray squirrel (*Sciurus*, class Mammalia, order Rodentia), eating a nut. Photograph by L. W. Brownell.

Another animal common in the forest in earlier times was the timber wolf, now almost extinct. It has been estimated that there was one wolf for every square mile in Pennsylvania. Wolves were the chief enemy of the deer. Their speed, endurance, large jaws, and sharp teeth admirably adapt them to be the marauders of the forest. The wolf is a flesh eater. In the summer it supports itself chiefly on smaller mammals such as mice, rabbits, and woodchucks. In winter, however, when these are in hiding, it turns to the deer whose escape is then made more difficult by the deep snow and the freezing over of the ponds. The wolf usually catches the deer by tearing the tendons of one of the hind limbs.

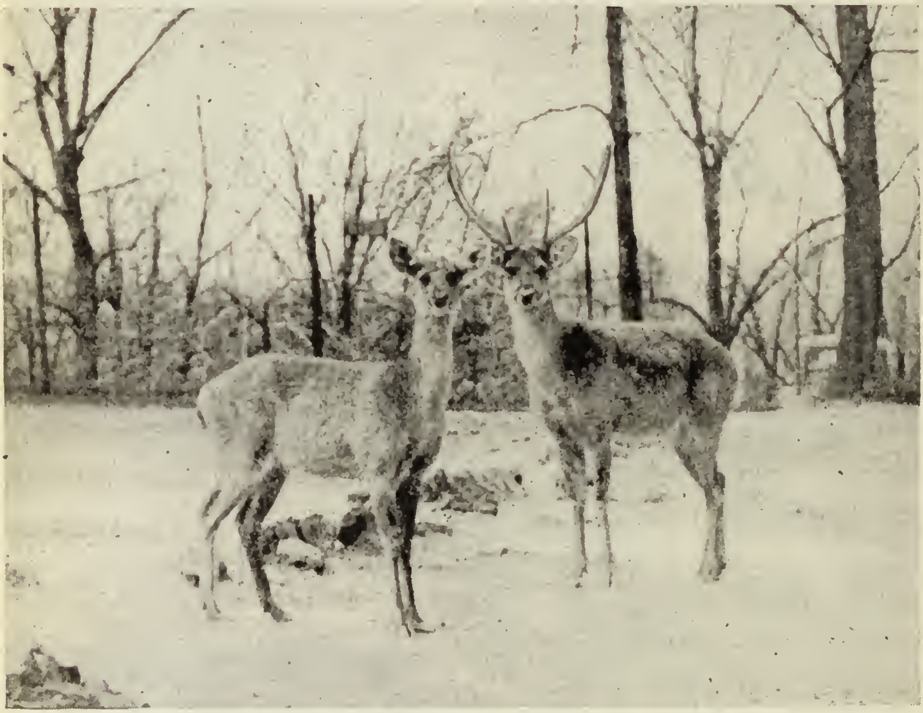


Fig. 39:13 Virginia deer (*Odocoileus*, class Mammalia, order Artiodactyla). Photograph by J. W. Mavor.

The black bear is another large forest mammal which has survived in the less disturbed forest areas and especially in the national park forests. Bears are classified as flesh eaters but they eat almost anything: berries, roots, honey, ants, fish, small mammals, and even birds. They do most of their feeding in the summer for when winter comes they find a hollow tree or a cave and go to sleep.

The birds of the forest find their food either on the ground or in the trees. Woodpeckers live in trees and dig insects out of the bark. Most of the common species are permanent residents of the forest but some migrate irregularly. The commonest and best known in the East is the flicker (Fig. 39:14), called by a number of other names including "golden-winged woodpecker," best known not only because of his striking coloration but also on account of his noisiness. Woodpeckers have high shoulders, long bodies, and stiff tails, the latter used to prop the body against the tree while the strong muscles of the neck and shoulders thrust the beak through the bark and wood. Like most woodpeckers the flicker usually makes its nest in a hole in a tree trunk which it digs with its beak. Besides the insects which he digs out of the bark and wood of trees this woodpecker, like many other birds, feeds on nuts and seeds.

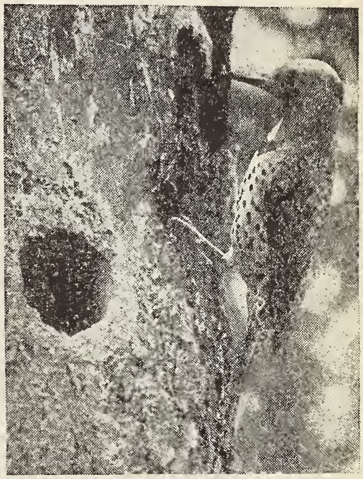


Fig. 39:14 A common forest bird, a flicker (*Colaptes*, class Aves, order Piciformes) approaching its nest hole in the trunk of a tree. Photograph by L. W. Brownell.

Other permanent residents of the forest are the chickadees (Fig. 3:26). These are typical perching birds, small and sparrowlike. They are more often noticed in the winter when there are not so many other birds about and the leaves are off the trees. Chickadees are useful birds living chiefly on insects. They destroy large numbers of moths and caterpillars, including tent caterpillars, in the summer and insect eggs during the winter. Their nests are made in hollows in trees. Often the abandoned nest of a woodpecker is used.

The wood pewee or pewee flycatcher is an example of one of the summer visitors of the forest. This small insect-eating bird comes in the spring and in the fall leaves for South America where he spends the winter. He prefers the shade of the forest and the tops of high trees. In the spring many different kinds of birds visit the more open parts of the forest to eat the berries on the shrubs.

Just as there are carnivorous mammals to eat the smaller animals of the forest so there are also carnivorous birds — the hawks and the owls. Both these types of birds are provided with sharp, curved talons and short, strong, hooked beaks. Hawks are active during the day and usually migrate to the South for the winter. Cooper's hawk, sometimes called the chicken hawk, roosts and nests in the forest although he may do a good deal of his hunting in the open. The speed with which he approaches his prey has given him the name "blue darter." He preys upon all kinds of birds, some as large as himself, and many small mammals including rabbits and squirrels. The nest is usually in a tall tree in some secluded spot and is frequently occupied for a number of years in succession. Owls are active at night. Their soft loose plumage makes their flight and movements noiseless. Their large eyes directed forward enable them to hunt in the dark. During the day they remain concealed. The great horned owl prefers the deep forest and comes out only to hunt. He is very fond of rabbits but also preys on grouse and will take a chicken. The eggs are laid early in the spring in a hollow tree or in an old hawk or crow nest.

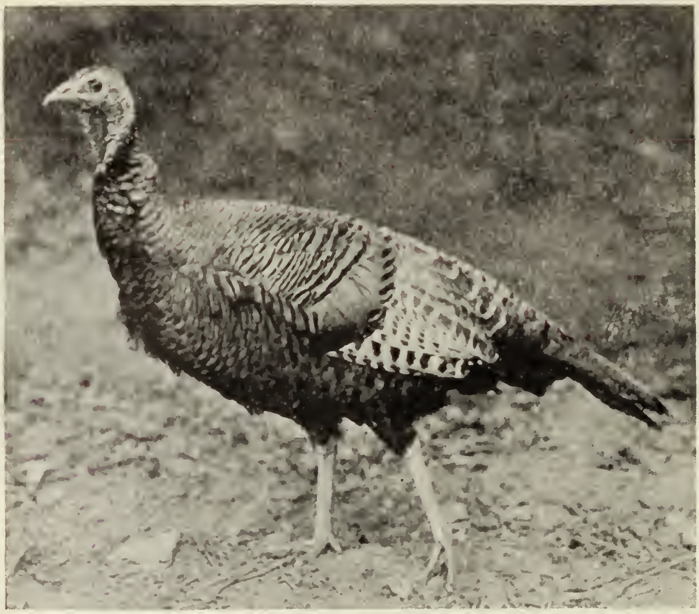


Fig. 39:15 Wild turkey (*Meleagris*, class Aves, order Galliformes), female. Photograph by L. W. Brownell.

The wild turkey (Fig. 39:15) is a good example of a permanent resident which lives mainly on the ground. It is a relative of the domestic fowl and like it has feet adapted for scratching and perching and a bill adapted for eating seeds and hard fruits. When America was discovered, the entire forested region from Canada to the Gulf of Mexico was inhabited by great flocks of wild turkeys. They are not good fliers, but their large size insures them from attack by the smaller forest animals while their protective coloring enables them to hide in the underbrush from their larger enemies such as the timber wolf. Their scratching feet enable them to find food beneath fallen leaves and twigs. When the snow comes and covers the ground, turkeys take to the trees and shrubs and feed on buds.

It thus becomes evident that a deciduous forest is a very intimate and intricate community containing innumerable relationships between plants, between plants and animals, and between animals. Through their interrelationships the abundance or scarcity of any species influences other species and through them the forest as a whole. Every animal and plant has its place or niche in the forest, and nothing is out of place except when something occurs to upset the balance. It sometimes happens that a species of plant or animal is introduced into a community, while its enemies are not simultaneously introduced. The introduced species then becomes numerous. When the community is free from outside influences such as that of the lumberman or the hunter, an equilibrium exists and the numbers of each kind of plant or animal remain approximately the same. This is due to the food cycle which is represented in Fig. 39:16. In the center of the figure are the green plants since they are the primary source of food.

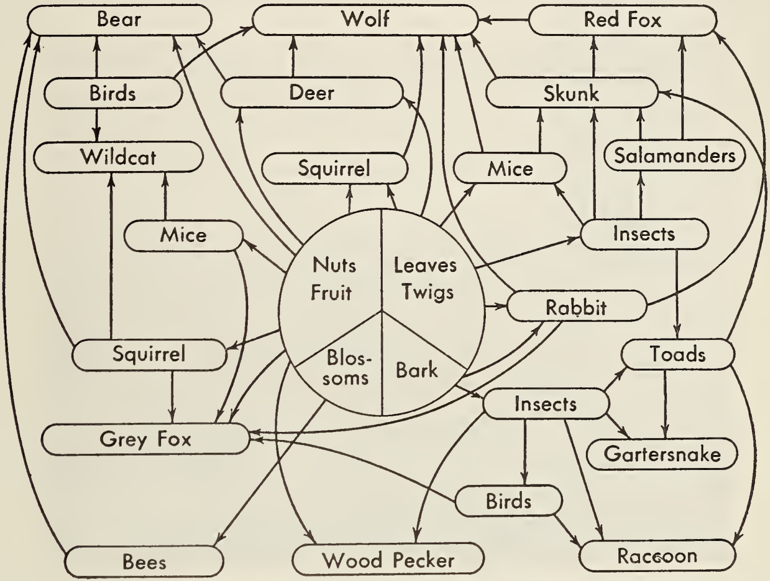


Fig. 39:16 Diagram to show equilibrium in food relations in a forest community. The arrows point from the animal or plant eaten to the animal which eats it. After Shelford from Shumway, *Textbook of General Biology* by permission of John Wiley & Sons, Inc.

B. LIFE ON A PRAIRIE OR GRASSLAND

West of the deciduous forest and extending westward to the Rockies, northward into Canada, and southward to the Gulf of Mexico are the great plains or prairies formerly covered with grass, now mostly cultivated land. In general the prairies are regions of less rainfall (20 to 40 inches per year), wider extremes of temperature (– 50°F in winter in lower Canada and 120°F in summer in the southern United States), and deeper soil than the forests. Moisture tends to sink deeper into this deeper soil. As a result of this and the lesser rainfall the surface of the land remains relatively dry. Characteristic of the prairie and largely responsible for the other forms of life existing there are various kinds of grasses and the absence of trees. Grasses are adapted to the relatively dry climate of the prairie by their narrow leaves and long branching fibrous roots. The fact that the part above ground, i.e., leaves and stem, dies down adapts them to the cold winters that follow the warm summers on the great plains (Fig. 39:17).

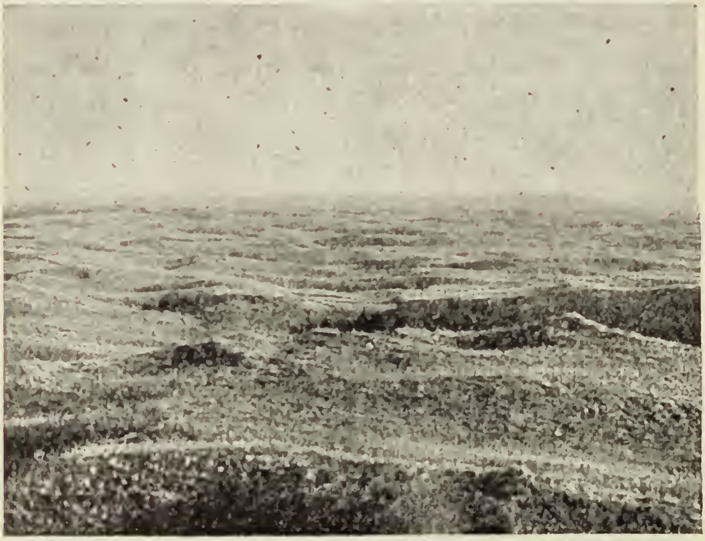


Fig. 39:17 View of a prairie. Mixed prairie in the sand hills of Nebraska, dominated by tall prairie grasses. From Raymond J. Pool, *Basic Course in Botany*, Ginn and Company.

The numerous species of grasses which occur over the prairies may be grouped into two main types — the tall grasses and the short grasses. In the eastern and more humid regions of the prairie the tall grasses are more abundant. Common species are speargrass, bluestem, dropseed, and wheat grass. In the western and drier portions of the prairie, known as the Great Plains, short grasses are more abundant. Common species of these are the buffalo grass and grama grass. These low grasses form a tough sod which may be continuous over large areas.

Mixed with the grasses and benefiting from their soil-forming ability are other herbs. Some of these, such as the ground plum, the false indigo, the bird-foot violet, and the spiderwort bloom in the spring, others like the sunflower bloom in midsummer, while various species of goldenrod, asters, wormwood, and ironweed flower in the late summer or autumn.

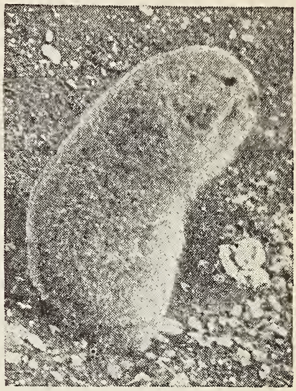


Fig. 39:18 A typical rodent of the prairies, a prairie dog (*Cynomys*, class Mammalia, order Rodentia) on the lookout near its hole. Photograph by J. W. Mavor.

Conditions on a prairie are very different from those in a forest. This is especially the case for the larger and medium-sized animals. There is no shelter on the prairie to protect them from the blazing sun of summer or the driving storms of winter; no trees for them to climb or hide behind when pursued by an enemy. To escape they must either run away or burrow in the ground. Prairie animals are therefore usually good runners or good burrowers. On the level land a carnivore can see its prey at a great distance; and the prey, too, if it is on the alert can see its enemies. Hence prairie animals usually have big keen eyes which are directed sidewise so that between them they can cover a wide field. The burrowing animals of the prairie, when out of their burrows, often sit upright so that they can get a better view. Sounds travel far on the prairie, and many prairie animals show an adaptation to this in their large ears with which they are able to pick up warning sounds. Many prairie animals are gregarious. By uniting in herds or flocks they can better protect themselves from enemies and by having sentinels always on the lookout they can more readily get warning of danger. Protective coloration is well developed in prairie animals.

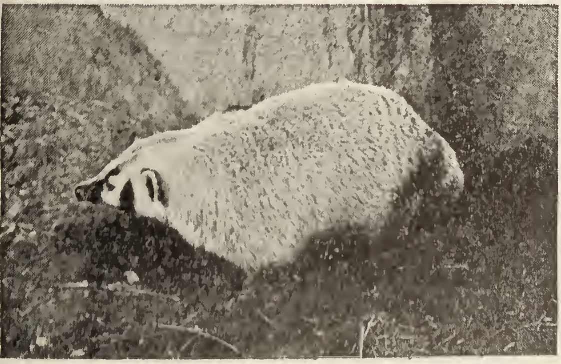


Fig. 39:19 A badger (*Táxidea*, class Mammalia, Order Carnivora). Photograph by the U. S. Bureau of Biological Survey.

The most characteristic small mammals of the prairies are the ground squirrels and their relatives. These animals burrow under the ground, making intricate mazes of tunnels. They feed on insects, grass, seeds, berries, roots, and herbage. Like most of the animals of the prairie they get all of the water they need in their food and rarely if ever drink. In their burrows they store up food which they eat in the spring after they have come out of their winter hibernation.

Familiar objects on the great plains are the prairie dogs (Fig. 39:18), not dogs at all but actually a kind of ground squirrel. One of their "towns" may cover 100 or more acres and consist of numerous mounds, each one the entrance to a tunnel which may go down 10 or 14 feet to a burrow. The animals are active during the day and prefer the bright sun. One or more of their number act as sentinels and the whole town takes to its burrows when warned of the approach of an enemy. They eat almost any vegetable material, root, stem, leaves, or fruit, and soon strip the area occupied by their towns of all vegetation.

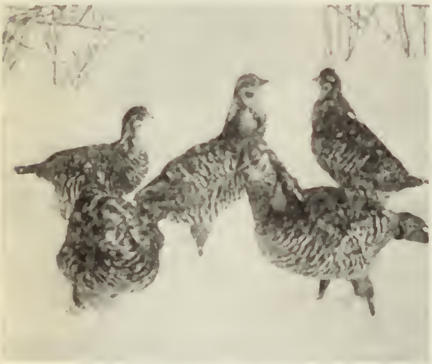


Fig. 39:20 Prairie chickens (*Tympanuchus*, class Aves, order Galliformes). Photograph by the U. S. Bureau of Biological Survey.

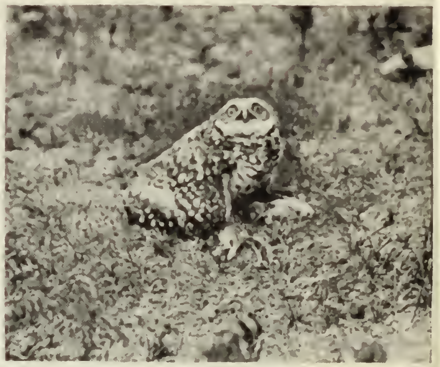


Fig. 39:21 A burrowing owl (*Speotyto*, class Aves, order Strigiformes). Note the large feet and the small head, both adaptations for burrowing. Photograph by the U. S. Bureau of Biological Survey.

Another characteristic rodent of the grassland is the prairie meadow mouse, or vole. These animals make tunnellike passageways with well-worn paths in the heavy undergrowth. They are active only at night. They feed on the vegetation and eat all parts of the plants but they also eat insects, especially grasshoppers and beetles. During the winter they remain active, moving over the surface of the snow. They are exceedingly prolific, a single pair producing numerous litters in a year. The prairie meadow mouse is fed upon by almost all the carnivores of the prairie — coyotes, badgers, hawks, owls, and snakes.

The badger (Fig. 39:19), whose fur is used in coats and shaving brushes, is well adapted to live in the grassland. Unlike many carnivores he is heavily built and adapted for burrowing, with a small pointed head, a stout flat body, powerful front legs, and long claws. He hunts in the burrows of other animals, digging out ground squirrels and prairie dogs, usually in the evening. In the northern part of his range he hibernates during the winter.

The prairie chicken (Fig. 39:20), once abundant but now unfortunately quite rare, is a good example of a bird of the grassland. As its name implies, it is somewhat like a chicken. Its mottled coloration makes it almost invisible in the grass. Its food in the spring and early summer is chiefly made up of insects. As the summer advances and the grass seeds ripen, it turns to these and feeds almost exclusively on them. In the fall of the year the birds gather in flocks in and under the low shrubs and trees that border the rivers and streams of the prairies where they stay during the winter, feeding on berries and seeds.

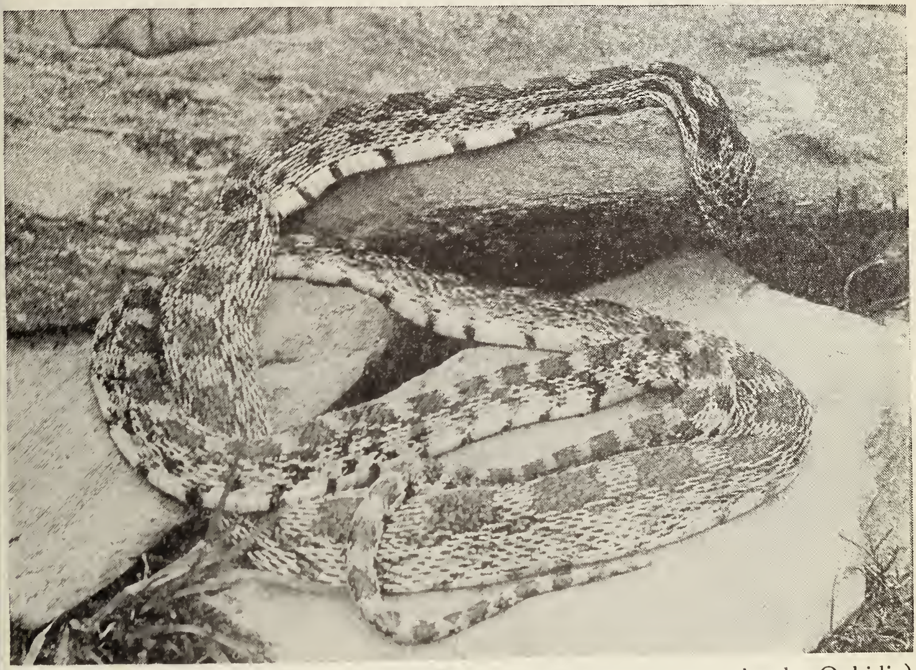


Fig. 39:22 Bull snake (*Pituophis*, class Reptilia, order Squamata, suborder Ophidia), a common snake of the prairies. Photograph by the New York Zoological Society.

The prairie horned lark is a relative of the European skylark of poetic fame and is common on the prairies in winter. It spends the summer in Newfoundland and northern Canada and comes to the prairies in flocks in the autumn. While feeding the birds of a flock scatter but when they take flight the flock unites. Like many prairie birds they sing while on the wing.

Even some of the prairie birds take to burrows like other animals of the grassland. The burrowing owl (Fig. 39:21) makes its nest in a burrow, often using one formerly occupied by a prairie dog. The owls live on the outskirts of the towns of the prairie dogs and feed on their young but will also eat lizards, insects, and other small animals. Like many grassland animals the burrowing owl has long legs, adapted not only to burrowing but also to running on the ground, and like many burrowing animals it has a rather small head.

Snakes find a livelihood on the prairie eating prairie dogs, gophers, and other small rodents, and the eggs of birds. One of these is the bull snake (Fig. 39:22). This is one of our largest snakes, reaching a length of nine feet. It is, however, a harmless and indeed a very useful reptile destroying many small animals destructive to crops, going into their burrows and swallowing them whole. It also eats birds' eggs, swallowing them intact and breaking them by contracting its throat muscles.

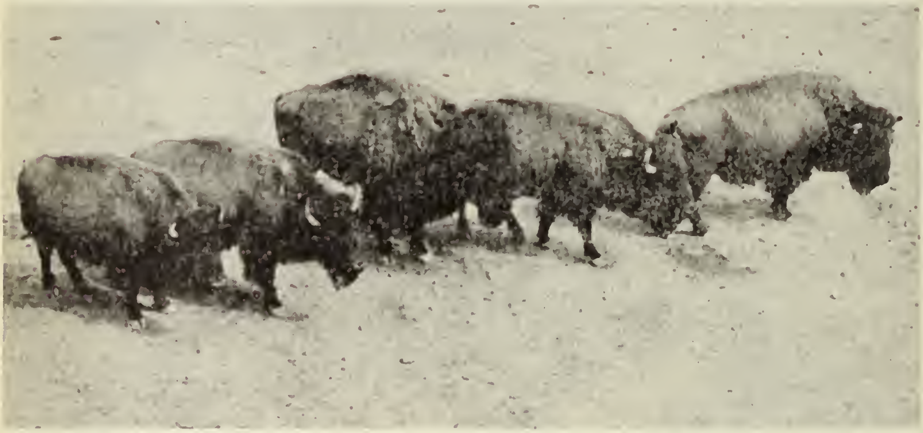


Fig. 39:23 A small group of American buffalo (*Bison,* class Mammalia, order Artiodactyla). Photograph by J. W. Mavor.

Frogs and salamanders are rare on the open prairie, their moist skins and aquatic breeding habits making them unfit for the dry climate.

Insects, on the other hand, are numerous, especially plant-eating insects such as grasshoppers, leaf hoppers, beetles, plant bugs, and bees of which there are many species. Snails, millipedes, and earthworms are rare, chiefly because of the lack of moisture.

Most of the larger animals of the prairie are ungulates, or hoofed mammals, which feed on the grasses. Grazing animals must be able to grind up and digest the hard leaves. The grinding is done by the back teeth (molars and premolars) which are large and ridged on top. Their work is facilitated by the long jaws which can be moved sidewise and back and forth as seen when the familiar cow is chewing its cud. The stomachs of such animals are usually somewhat complicated and divided into separate chambers, each adapted to carry out some special part of the digestive process. The legs are usually long, and the muscles of the upper parts connecting them with the body strongly developed for running. The number of digits is usually reduced (the horse has only one and the bison but two on each foot) and the digits carry hoofs in place of claws. A special defensive weapon in the form of horns has been developed in some species.

All of these adaptations are well shown in the buffalo (Fig. 39:23). Buffaloes roamed in great herds over the prairies before the white man came. They are now extinct in the wild state and survive only in semi-domestication on protected ranges. The less-populated prairie lands of Africa are still the home of great herds of zebras, gazelles, and wildebeests.

There are several species of prairie wolf, usually known by the Spanish-American equivalent, coyote. Coyotes are smaller than timber wolves. They live in underground dens often of considerable size. During the summer months they feed chiefly on ground squirrels, prairie dogs, and mice. In the winter when these animals are in their burrows they turn to birds and larger animals.

Life on a prairie is centered around the dominant plants, the grasses, since they are the main source of food for all the other organisms which make up the community. All of these organisms must be adapted not only to the physical conditions which exist on the prairie but also to obtain their food there and to resist or avoid their enemies. As in the case of the forest there are food chains — plants providing food for herbivores, and herbivores food for carnivores. Each species fits into a particular niche in the community.

3. LIFE IN FRESH WATER

The proportion of the earth's surface covered with fresh water is small compared with that occupied by the oceans or the land. Nevertheless plants and animals of the fresh water are of great interest on account of their many adaptations to the peculiarities of their environment. A permanent fresh-water pond is chosen for study. In general a permanent pond contains a greater variety of life than one which dries up in the summer. Physical conditions have a marked effect on the life of a pond. On the whole, organisms which live in water get less light. Water absorbs light to a much greater extent than air, and natural bodies of water usually contain many suspended particles which add greatly to this absorption. Less light is therefore available to the submerged green plants for photosynthesis. While the atmosphere contains about 20 per cent oxygen and only about 0.03 per cent carbon dioxide these gases dissolve in water in very different proportions. The oxygen content of pond water is usually under 5 cubic centimeters per liter or less than a half of 1 per cent by volume while there may be over 10 cubic centimeters of carbon dioxide per liter or more than 1 per cent. The proportion of the two gases depends to a considerable extent on the amount of green vegetation and animal life in the pond. Under normal conditions green plants tend on the whole to take carbon dioxide from, and to add oxygen to, the water. The oxygen given off by green plants in the process of photosynthesis is often seen in the bubbles which collect on the leaves of submerged plants or in masses of floating pond "scums" (*Spirogyra* and other genera). Because bacteria and other organisms of decay may use most of the available oxygen, polluted waters often contain little or practically no oxygen and so are unable to support many kinds of animal life. The chemical composition of fresh water varies with the kind of soil or rocks over which it flows and this in turn affects the organisms. The amount of mud or other fine suspended material, by determining

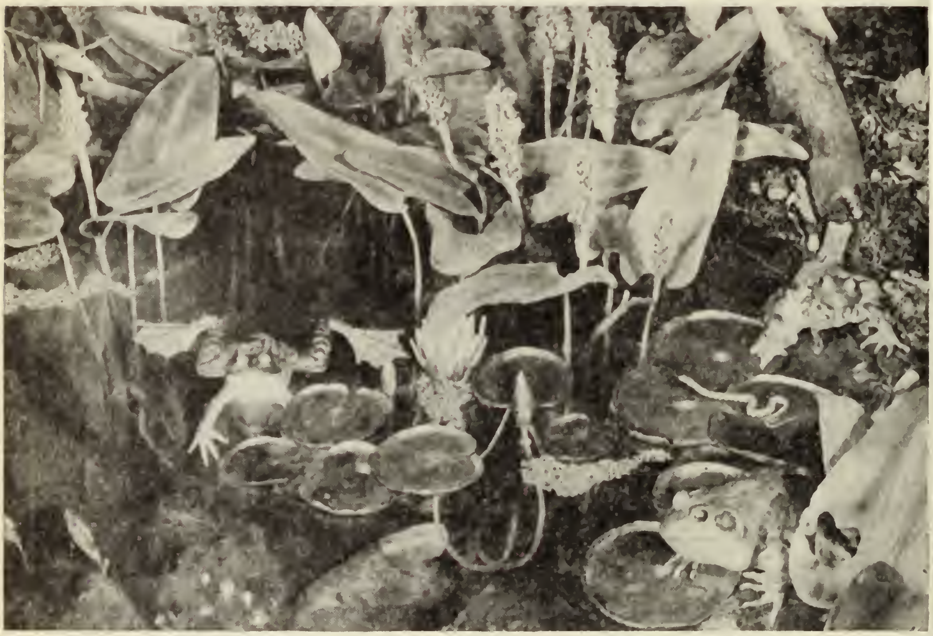


Fig. 39:24 Pond life. On the lily pad (*Castalia*, order Ranales) in the foreground is a bullfrog (*Rana catesbiana*, class Amphibia). In the center a leopard frog (*Rana pipiens*) is resting at the surface of the water. Pickerel-weed (*Pontederia*, class Monocotyledoneae) thrusts its large leaves and flowers out of the water near the shore. A small water snake (class Reptilia, order Squamata, suborder Ophidia) crawls over some lily pads behind the bullfrog. Another bullfrog on the shore is eating a water snake. Photograph of part of a habitat group. Reproduced by courtesy of the American Museum of Natural History.

the penetration of sunlight, affects not only photosynthesis in plants but also affects the movements and habits of the animals.

Around the fringe of a fresh-water pond in the shallow water are cattails with their brown spikes, bur reeds with their fluffy balls of flowers, bulrushes with their long narrow leaves and the pickerelweed (Fig. 39:24) with its large pointed leaves like great spear heads. Beyond this zone of plants which live partly in and partly out of water the surface of the pond is covered to a varying distance, depending upon the depth, by the large flat floating leaves of the delicate white water lily or the coarser yellow pond lily or spatterdock. The large, flat, floating leaves of these plants are obviously an adaptation to life in this part of the pond. Further from the shore where the water is deeper the plants are either totally submerged, preferring as it were to retain their roots in the muddy bottom, or float freely on the surface. To the former category belong the species of pondweeds and the fresh-water eelgrass, a pest to those who try to swim or canoe along the shore. The long flexible leaves of the eelgrass move with the water and hence are not torn by waves. Another submerged plant is *Elodea*, a form often used in the laboratory. The buds of submerged plants, like *Elodea*, are not covered with scales as those of land plants are. Such scales serve to prevent drying in land plants and would have no use in water plants. To the freely floating plants belong the peculiar duckweeds (Fig. 39:25) which consist of little green discs ¼ inch or less in diameter but which are in reality full-grown flowering plants as are all of the species named so far.

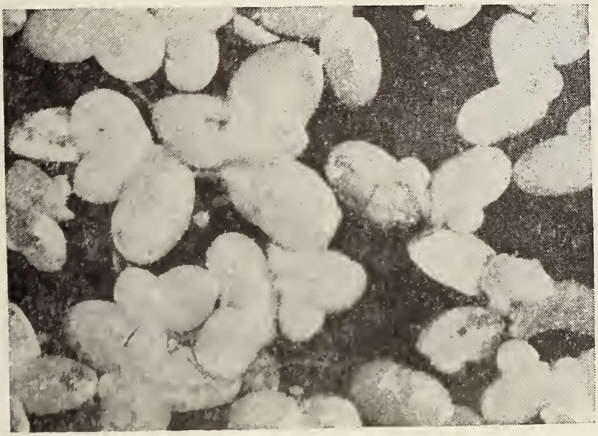


Fig. 39:25 Duckweed (*Lemna*, class Monocotyledoneae, order Arales, family Limnaceae) floating on the surface of a pond. Photograph by J. W. Mavor.

One may ask how it happens that flowering plants are found in ponds when their stems, leaves, and roots and their method of reproduction by means of pollen and seed show that their structure is of the type found in land plants. The answer is that their ancestors not very far back were land plants; but that they invaded the water, perhaps because they were crowded off the land, and became readapted to it without, however, changing the fundamental plan of their structure or methods of reproduction. That this readaptation occurred in most cases relatively recently

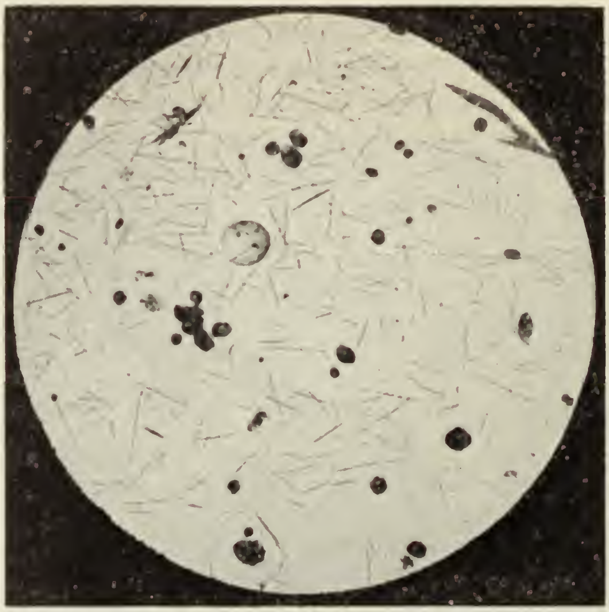


Fig. 39:26 A sample of fresh-water plankton from a small lake. Note the spherical colony of *Volvox* (phylum Thallophyta, subphylum Algae, class Chlorophyceae). Most of the organisms are either desmids or diatoms. Photograph by J. W. Mavor.

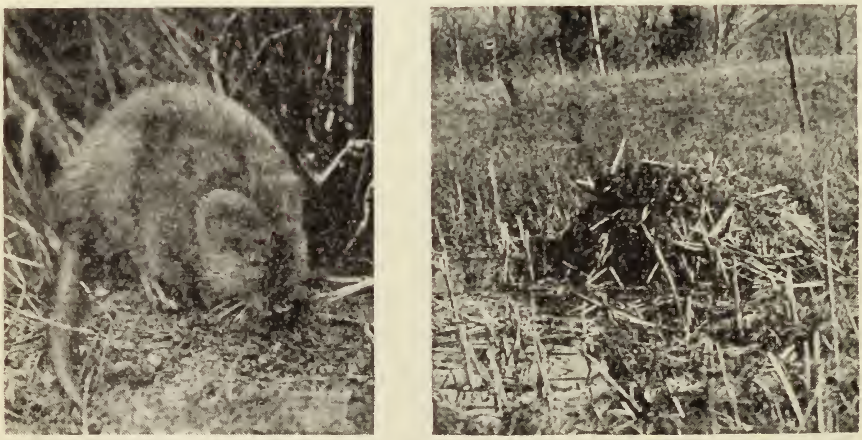


Fig. 39:27 On the left a muskrat (*Fiber*, class Mammalia, order Rodentia). Photograph by L. W. Brownell. On the right a muskrat house. Photograph by J. W. Mavor.

and independently is shown by the fact that many different orders of flowering plants contribute to the aquatic life of ponds.

Among the floating plants may be found water fernworts, curious relatives of the familiar ferns but rather different from them in appearance, and liverworts, plants related to the mosses.

With very few exceptions the algae which occur in fresh water are either blue-green algae or green algae. Filamentous plants of the latter class may be seen at or near the surface forming dull green masses buoyed up by bubbles of oxygen. Freely floating microscopic forms (Fig. 39:26) tint the water green or brownish green. Branched forms cover the submerged stems of the larger plants with a hairy coat. Stoneworts, delicately branching green algae, often called candelabra plants, grow up from the bottom which is partly covered by blue-green algae and diatoms.

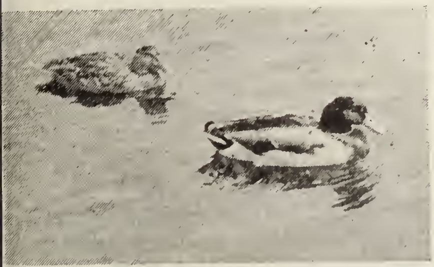


Fig. 39:28 Mallard ducks (*Anas*, class Aves, order Anseriformes). Male, right, with ornate plumage. Female, left. Photograph by L. W. Brownell.

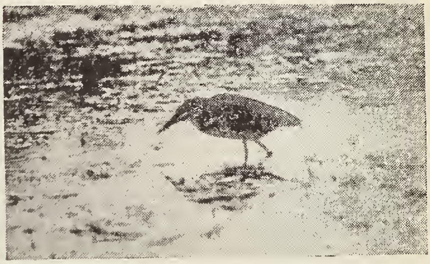


Fig. 39:29 A green heron (*Butorides*, class Aves, order Ciconiformes). Photograph by the U. S. Bureau of Biological Survey.

The animal life of a pond is no less peculiar than the plant life. The two commonest water mammals are the muskrat and the mink. The muskrat (Fig. 39:27) is about the size of a cat and has the general appearance of a large mouse or rat. It is, however, adapted to an aquatic existence; the hind feet are partly webbed, the tail is flattened vertically to act as a rudder, and the fur sheds water. The muskrat makes his house in a marsh in the form of a mound built of the roots and stems of rushes, cattails, and other plants. The house may reach a size of 5 feet wide and 2 feet high and contains a little room with a dry floor above water level. Sometimes instead of being built in water the house is made by burrowing into the bank of a pond. In either case the entrance is under water. Muskrats feed on roots and stems but will eat a frog or fish if it comes their way. Minks are at home either on land or in water. They are long slender animals and are entirely flesh eating, living while on land on mice and small birds and while in the water on fish, crayfish, and other aquatic animals which they catch with agile snakelike movements.

The most numerous and characteristic of the water birds are the ducks. Their boatlike bodies and webbed feet placed posteriorly so as to act most efficiently as paddles make them well adapted to move over the surfaces of ponds and lakes. Game ducks like the mallard (Fig. 39:28), the flesh of which is highly prized, feed on plants such as the fresh-water eelgrass. The flesh of the fish-eating ducks has a disagreeable taste. Sandpipers run along the sand or mud at the water's edge searching for titbits. Occasionally one may find a colony of black-crowned night herons or a little green heron (Fig. 39:29) and from a distance watch some of them wading with their long legs and catching fish in their long sharp beaks. Kingfishers prefer the banks of streams where they watch for their prey from an overhanging bough and guard their fishing ground from encroachment by other members of their species; but they may choose a pond or a marsh. Hovering overhead may be a marsh hawk, for wherever there are plant eaters there are also flesh eaters to devour them.

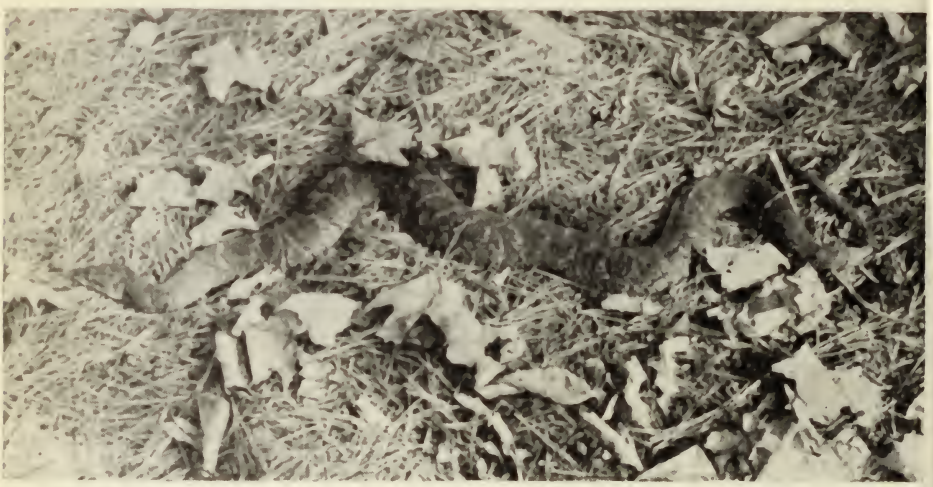


Fig. 39:30 A water snake (*Natrix*, class Reptilia, order Squamata, suborder Ophidia) resting after a meal. Photograph by J. W. Mavor.

As one approaches almost any pond one looks for turtles, especially if there are logs about. One of the commonest species is the painted turtle (Fig. 3:25). Another turtle common in ponds and marshes is the snapping turtle.

Turning to snakes, one of the commonest in eastern North America is the common water snake (Fig. 39:30), a dull olive creature which reaches a length of 3 or 4 feet. These reptiles lay their eggs on land.

The commonest frog of the ponds of eastern North America is the eopard frog, the tadpoles of which usually occur in large numbers during the late spring and summer, at the end of which time they change nto the adult. Bullfrogs and their tadpoles are not uncommon. The atter do not change into frogs until the second or third year. Tadpoles are usually vegetable feeders while most frogs feed on insects.

Adults of the spotted newt are often common in fresh-water ponds. After changing from a tadpole resembling that of a frog and coming out of the water onto the land, this tailed amphibian spends its youth in the forest as a bright vermilion-colored salamander. Later it changes its color to a dull green and takes again to a fresh-water pond where it breeds.

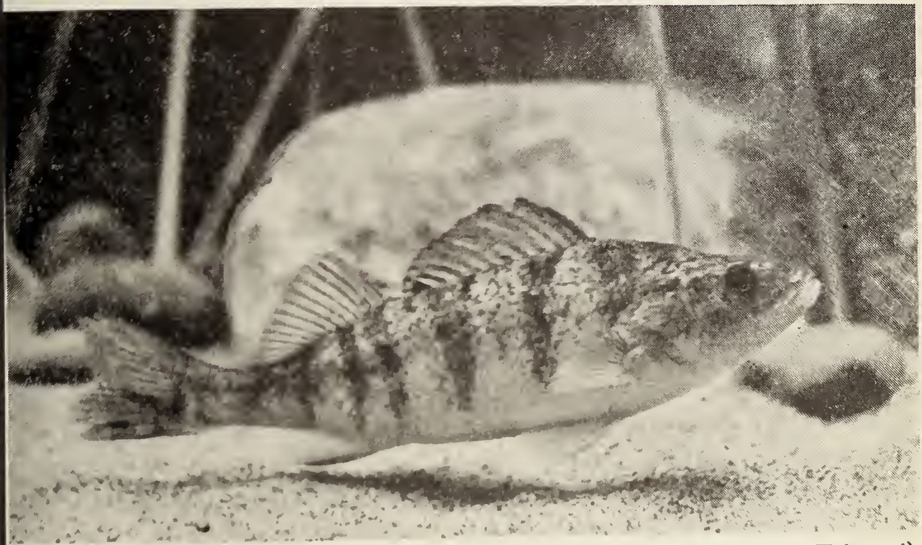


Fig. 39:31 A perch (*Perca*, class Osteichthyes, subclass Actinopterygii, order Teleostei). Photograph by John G. Shedd Aquarium, Grant Park, Chicago, Illinois.

One is inclined to think of fish as the most important inhabitants of a pond. The yellow perch is often common in fresh-water ponds and small lakes (Fig. 39:31). It feeds on worms, insects, and smaller fishes. Perch are active during the winter and are often caught through the ice. There are many kinds of sunfish, or "pumpkinseeds." Most of them feed near the surface on floating or swimming organisms. More interesting to the fisherman are the small-mouthed black bass and the large-mouthed black bass. The small-mouthed black bass is the smaller fish. Both species are carnivorous and feed on other fish. All of the fish mentioned above are well protected by spines and like most fishes are light colored on the under side which makes them less conspicuous to an enemy looking up from below. Several species of catfish occur in fresh water, the most widely distributed of which is probably the common bullhead. The name "catfish" owes its origin to the barbels or "feelers" which surround the mouth and are kept constantly in motion as the fish swims leisurely over the bottom of the pond. Catfish are omnivorous and feed during both day and night.

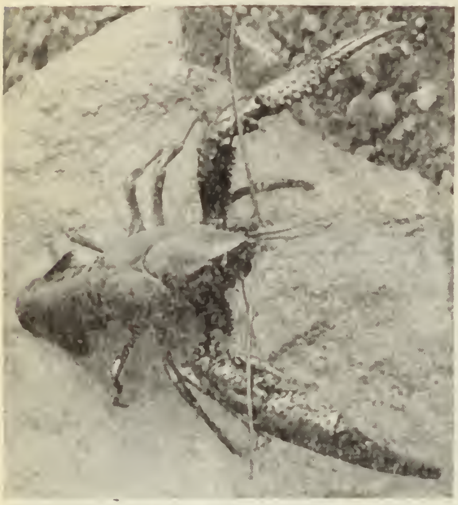


Fig. 39:32 A crayfish (*Cambarus*, phylum Arthropoda, class Crustacea). Photograph by L. W. Brownell.

The most conspicuous and the more active of the small animals of a pond are the arthropods or jointed-legged animals. One group of these is the crustacea to which the crayfish (Fig. 39:32) belongs. This animal closely resembles a small lobster and is one of our largest fresh-water crustaceans. It lives under stones and among the roots of aquatic plants, feeding on smaller animals. But the smaller crustacea are the more numerous, some of the commonest being water fleas, copepods, ostracods, scuds, and sow bugs. The water flea rows itself through the water with a pair of relatively enormous antennae. Copepods (the name means "oar-footed") are little fellows with large heads, tapering bodies, and a cyclopean eye. They dart about with tantalizing rapidity, the females carrying two large egg sacs, one on either side of the tail. Ostracods (literally "enclosed in a shell") are small egg-shaped animals which creep over the decaying vegetation. Scuds are little, laterally compressed crustaceans with arched backs which glide through the water and cling to plants. Sow bugs look like miniature armadillos and crawl rather than swim.

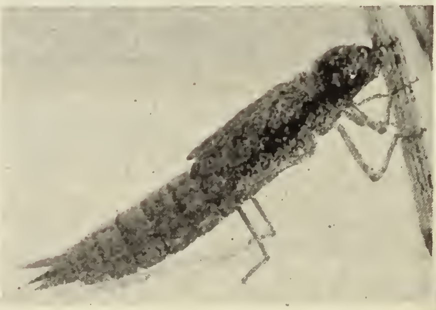


Fig. 39:33 Dragonfly nymph (class Insecta, order Odonata). Photograph by L. W. Brownell.

Usually the most conspicuous of the smaller animals in and around a pond are insects. Insects are primarily land animals which breathe air. Those which live in water have taken secondarily to this habitat and were evolved first as air-breathing animals on land, just as the flowering plants of the pond were first land plants. This is indicated by their mode of breathing which, like that of all other insects, is by means of air tubes. The insects which are found in ponds are usually in a larval or immature stage which is often quite unlike the adult which lives on land. Especially common are the young stages, called nymphs, of dragonflies (Fig. 39:33), quaint creatures with the lower part of the mouth (labium) hinged and modified to form a relatively enormous scoop with which they capture other small animals. The adult dragonflies (Fig. 24:9) are familiar objects in the vicinity of ponds during the late spring and summer. The larvae of various kinds of flies including mosquitoes and midges may also be common. Adult pond insects include: the water striders, or water skaters, curious long-legged creatures which run over the surface of the water, kept up by surface tension; back swimmers which hang from the surface with their heads downward and their long hind legs stretched out like oars; waterbugs like the giant electric-light bug which moves about among the vegetation devouring other insects and even young fish, and gets its name from the fact that it frequently leaves the water and is then attracted by electric lights; and the diving beetles.

Spiders and mites, each with four pairs of walking legs (insects have three pairs), are land animals but a few species have become aquatic and are found in ponds.

Two groups of mollusks occur in fresh water — mussels and snails. Fresh-water mussels or clams burrow in the sandy bottoms of small lakes, ponds, and the backwaters of streams. The snails crawl over the vegetation on which they feed. One kind which keeps near the surface breathes by means of "lungs" like a land snail and must come to the surface for air. Another kind breathes by means of gills and remains below.

The worms include leeches and the tube worms which live on the bottom in tubes from which their bodies project and wave about. Roundworms abound and planarians (Fig. 3:13) may be seen swimming through the water with a graceful undulatory motion, but this group of animals is usually more abundant in streams. Moss animals occur in fresh water; their colonies like large masses of jelly are often attached to floating vegetation. The fresh-water hydra (Fig. 2:7) attaches itself to aquatic plants. Its occurrence is somewhat irregular and seasonal but it is frequently not uncommon. In recent years fresh-water jellyfish have been recorded from a number of localities. Fresh-water sponges are found attached to submerged stems or dead logs.

Under the microscope a drop of pond water, preferably one taken from near the bottom or among the vegetation, shows a new and quite different world of life. Tiny wheel animalcules or rotifers (Fig. 3:15) move about among the filaments and leaves of the water plants. They are scarcely larger than some of the unicellular animals with which they may easily be confused. The latter are perhaps the most interesting of all the fresh-water creatures because they are so strange and different from those one is accustomed to see with the unaided eye. They will not be considered in detail here but it should be noted in passing that they are an important source of food for the other small animals of the pond and indirectly for the larger animals which feed on these smaller animals.

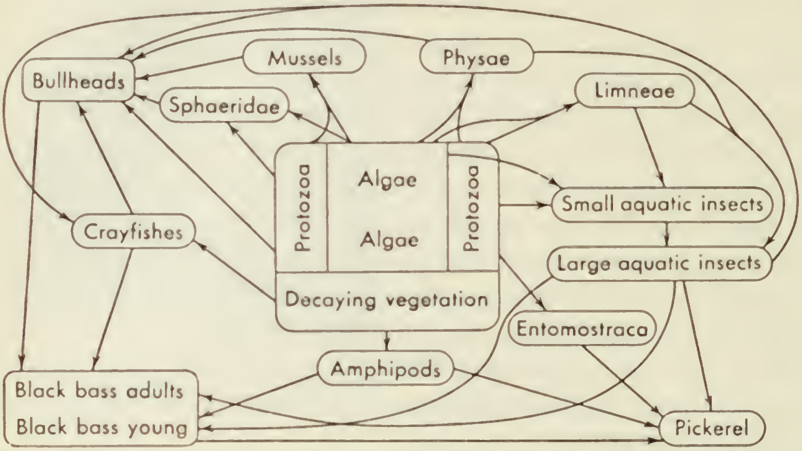


Fig. 39:34 Diagram to show equilibrium in food relations of a lake or pond community. The arrows run from the organisms used as food to those which prey upon them. The Sphaeridae, mussels, Physae, and Limneae are mollusks; the Amphipods and Entomostraca are crustaceans. After Shelford from Woodruff, *Foundations of Biology*, The Macmillan Company.

If a fine silk net is towed from a rowboat just below the surface a sample of the plankton of the pond or lake will be obtained (Fig. 39:26). By "plankton" is meant the animals or plants which live suspended in the water and which are either too small or lacking in the power of locomotion to move about extensively under their own power. The plankton will undoubtedly contain a number of species of desmids, one or more species of blue-green algae, and small crustacea and unicellular animals.

In a pond, as in a forest or on a prairie, there are intimate relationships between the different plants and animals. Food chains (Fig. 39:34) are maintained just as they are in the forest and on the prairie, and each species fits into a certain place in the community.

4. LIFE IN THE SEA

The sea may have been the first real home of abundant life. The sea contains a greater variety of algae and a greater variety of animal life han any other part of the world and it contains examples of all of the ost primitive forms of life. There is evidence that nearly, if not all, of he animals which now live in fresh water or on land came there from the ea and passed through the earlier stages of their evolution in the sea.

Striking features of the sea as an environment are the salt content f the water, the tides, and the ocean currents. The salt content of sea ater is about 3.5 per cent by weight of which 2.7 is common salt (NaCl). he effect of the tides is felt chiefly on the seashore and near the shore here the water goes (ebbs) and comes (flows). Ocean currents affect he distribution of floating organisms.

A. LIFE ON THE SEASHORE

The ebb and flow of the tides twice in 24 hours at varying times of he day or night creates a region along the coast called the **tidal zone** hich during low tide is part of the land and during high tide part of the ea. The plants and animals which live in this zone must either move ith the tide or be adapted to a sudden and violent change in their nvironment. The tides also cause currents to flow to and from and along he shore. In addition, the waves of the restless ocean pound every exosed promontory or strand.

Waves, combined with wind and rain, wear down the rocks of the oast, making of them first pebbles and later sand to be spread out in ea beaches. At the mouths of rivers and in protected bays, mud washed rom the land combines with the sand to form mud flats over which the ide may ebb and flow for miles. Thus the seashore provides many differnt types of habitat. Life on a rocky shore, a sandy beach, and a sand nd mud flat will be described.

(1) A ROCKY SEASHORE

The plants or animals which live on rocky shores (Fig. 39:35) within he tidal zone are usually either permanently attached to the rocks or are apable of temporary attachment. In this way they avoid being washed way by the tide or dashed to pieces against the rocks by the waves.

The most successful algae are the rockweeds or bladderworts (Fig. 9:42) which form the brown slippery carpet over the rocks of the tidal one familiar to those who have walked along the seashore. This is one f the brown algae, a group which is especially abundant on the seashore nd in the shallow water off shore. The tough thallus of the plant is overed with a thick, resistant cuticle which prevents it from drying up hen the tide goes out. The bladders, the contents of which are chiefly

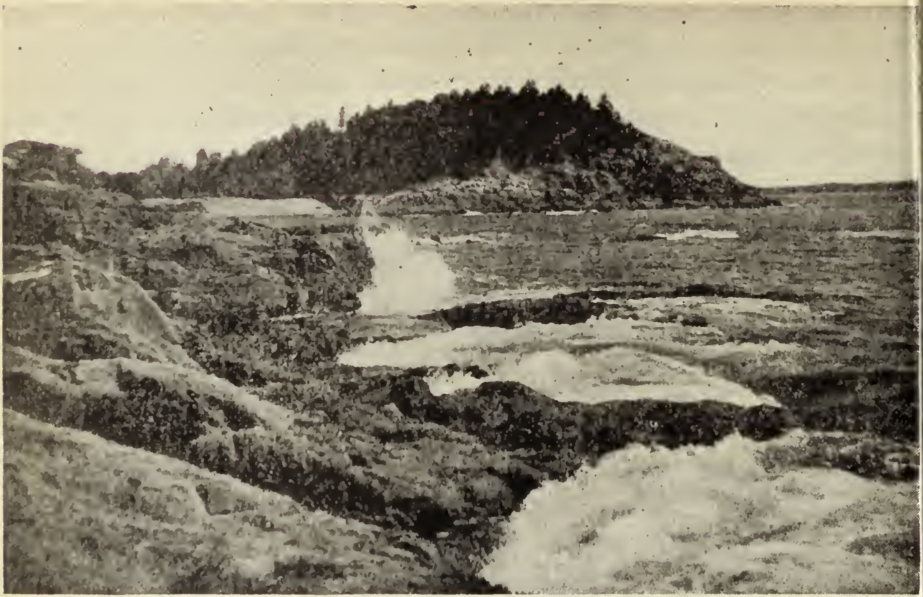


Fig. 39:35 General view of rocky shore, Mount Desert Island. Photograph by J. W. Mavor.

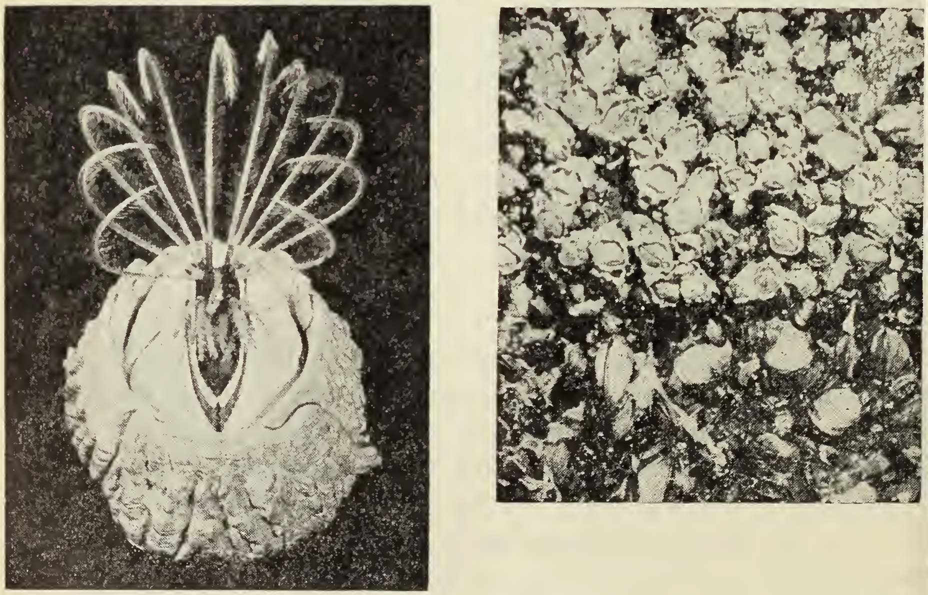


Fig. 39:36 On the left, a photograph of a model of a barnacle with its appendages thrust out, reproduced by courtesy of the American Museum of Natural History, New York. On the right, barnacles (*Balanus*, phylum Arthropoda, class Crustacea) and young mussels (*Modiolus*, phylum Mollusca, class Pelecypoda) are competing for space on a rock. Photograph by J. W. Mavor.

carbon dioxide gas, serve to float the otherwise rather heavy plant body. With the rockweed there often occurs, especially near where fresh water flows into the sea, a bright green, leaflike alga called sea lettuce or sea cabbage. Only a few of the higher plants are able to live in salt water and none of these occur on rocky shores.

Just below high-tide mark the more exposed rocks are covered with white barnacles (Fig. 39:36). The sharp-pointed, calcareous shells of these animals will cut deep into the flesh of the unwary bather. When under the water and not disturbed, the conical shells open and disclose the delicate plumelike appendages of a crustacean. These animals produce a free-swimming larva, not unlike that of a crab or lobster. The larva attaches itself by its back to a rock and forms a shell from which its appendages, now grown plumelike, are protruded. These appendages create a current of water which wafts microscopic plants and animals into its mouth.

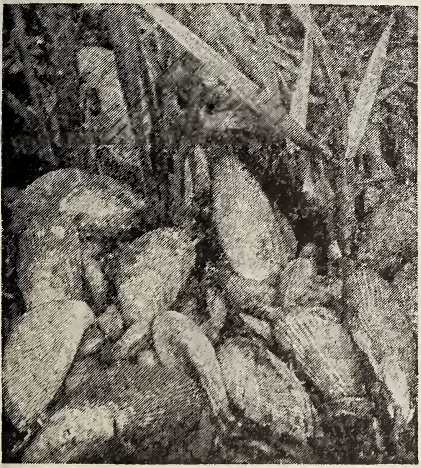


Fig. 39:37 A group of black mussels (*Modiolaria*, phylum Mollusca, class Pelecypoda). Photograph by L. W. Brownell.

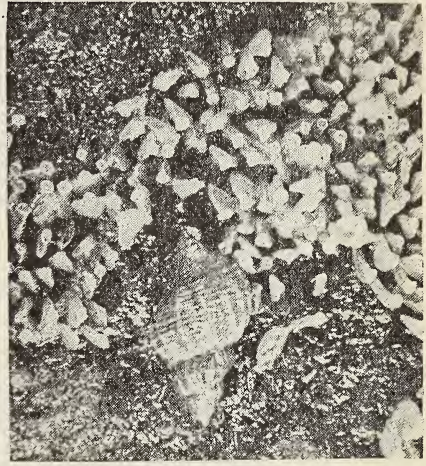


Fig. 39:38 An oyster drill (*Urosalpinx*, phylum Mollusca, class Gastropoda) in the act of laying eggs in capsules which show as the numerous little white flask-shaped structures in the picture. Photograph by J. W. Mavor.

Competing with the barnacles for "standing room" on the rocks are numerous small mussels (Fig. 39:37) attached to the rock by tangled masses of fine threads. When covered by the tide these bivalved mollusks open their shells and feed upon the microscopic animals and plants abundant in sea water. The sedentary life of mussels is no more peaceful than that of any of the other inhabitants of the rocky shore. The purple sea snail moves among them covering their shells with its large foot

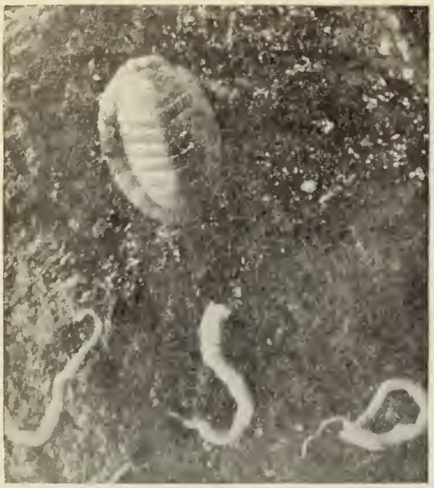


Fig. 39:39 A chiton (*Chiton*, phylum Mollusca, class Amphineura) crawling over a rock on which there are three tubes of segmented worms (*Hydroides*, phylum Annelida, class Chaetopoda, order Polychaeta). Photograph by J. W. Mavor.

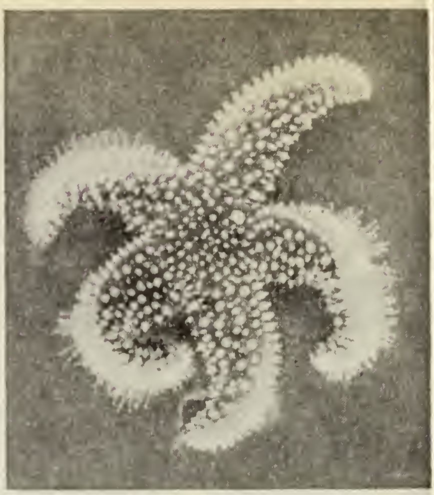


Fig. 39:40 A starfish (*Asterias*, phylum Echinodermata, class Asteroidea), viewed from the upper or aboral surface. Numerous fine white tube feet extend out from the arms. Photograph by J. W. Mavor.

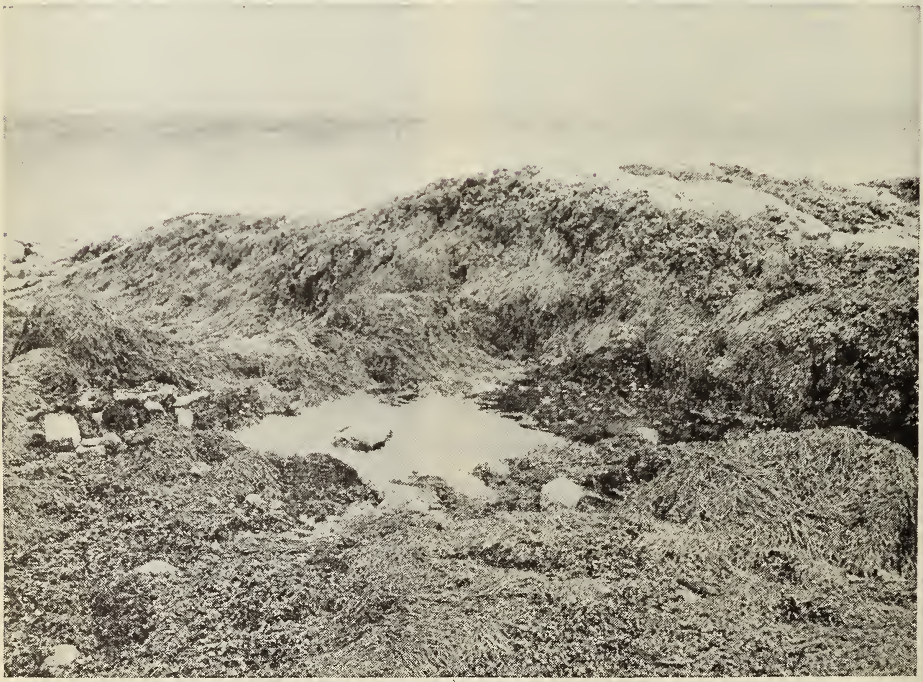


Fig. 39:41 A tide pool. The tide has receded and left the rocks covered with rockweed (*Fucus*). Photograph by J. W. Mavor.

vhich it can swell so as almost to cover its own shell too. With a sharp ilelike tongue or radula it drills a hole in a mussel shell and then sucks he soft body of the unfortunate victim through it. The natural home of he oyster is among the rocks although it is usually cultivated on sand and mud flats. It is also a bivalved mollusk, one of the valves being irmly cemented to a rock or stone and the other valve raised when the shell is opened. The oyster feeds much in the same way as the mussel.

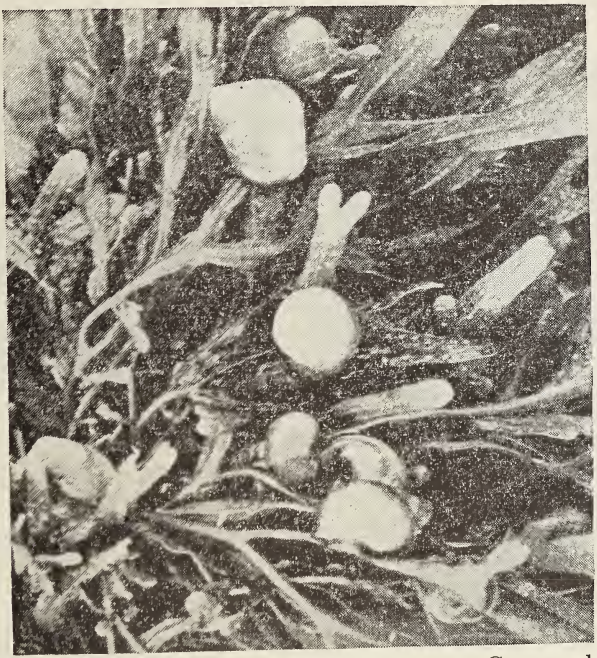


Fig. 39:42 Periwinkles (*Littorina*, phylum Mollusca, class Gastropoda) browsing on rockweed (*Fucus*). Photograph by J. W. Mavor.

Like the mussel, it has its arch enemy, the oyster drill (Fig. 39:38), which drills through its shell and enjoys a raw meal, anticipating the human epicure.

The little limpets, boat shells, and silver shells, although less numerous than the above, always arouse interest. They are snaillike creatures in which the shell, instead of being coiled like that of a snail, has the form of a low cone. The animals protect themselves from enemies and the weather by adhering firmly to the rock so that they appear at first sight to be a part of it. Somewhat similar in appearance are the chitons (Fig. 39:39), primitive mollusks with the shell made up of a series of bandlike plates. They also protect themselves by adhering firmly to the rocks so that only the shell plates are exposed.

Starfishes (Fig. 39:40) and sea urchins (Fig. 3:17) move about over the rocks but are capable of adhering firmly by means of their peculiar tube feet. Starfish feed on mussels, small fish, and almost any small animal they can catch. In the case of a mussel or other bivalve the struggle is one of endurance. The starfish attaches its arms to the mussel by its tube feet and gradually pulls the valves apart. Then the stomach of the starfish is everted, passes into the shell, and surrounds the soft body of the mussel or oyster. Here digestion takes place and the digested materials pass into the starfish. Sea urchins, a little larger than golf balls and about the same shape but with sharp spines radiating out in all directions, feed on the various plants and animals which cover the surface of the rocks. Surrounding the mouth of the sea urchin, which is on its under side, are five sharp teeth connected by muscles with a complicated skeletal structure known on account of its discoverer as "Aristotle's lantern." When feeding, these teeth cut out a circular piece of food which is pushed through the mouth and into the stomach.

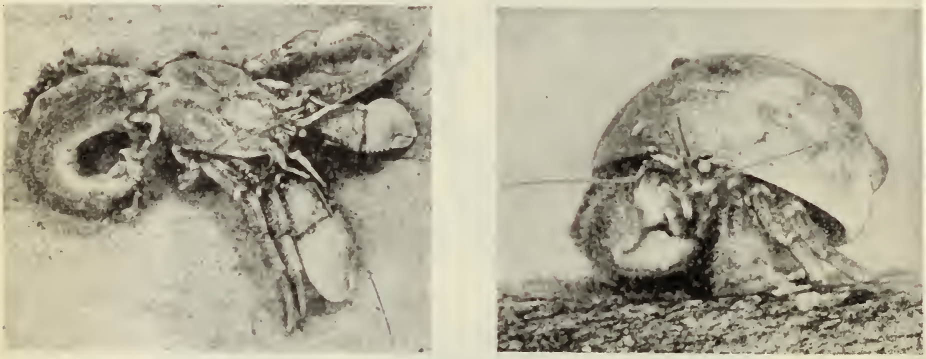


Fig. 39:43 A hermit crab (*Pagurus*, phylum Arthropoda, class Crustacea). On the left the crab is out of its shell and its long coiled abdomen shows. On the right the same crab is in its borrowed shell. Photograph by J. W. Mavor.

There is probably no more fascinating spot on the seashore nor one which offers a better opportunity to study shore life than a tide pool (Fig. 39:41). Here, sheltered from the waves and the going and coming of the tide, flourishes a busy and varied world of little creatures. Periwinkles or acorn snails (Fig. 39:42) adhere in clusters, feeding for the most part on the rockweed. Hermit crabs (Fig. 39:43) scurry about in the shells of periwinkles or other small sea snails, for they make no shells of their own and must find shells to fit their peculiar elongated and coiled bodies. Upon the shell of their adoption a colony of small and delicate hydroids makes its abode, disguising the shell and receiving in return protection and titbits from the crab — an interesting case of symbiosis or the living together of individuals of different species to their mutual advantage. Other hydroids abound attached to the fronds of seaweed. Also attached to seaweeds and at first sight somewhat resembling hydroids but really very different are moss animals (Fig. 3:16). In places the rocks are covered with incrusting sponges, bright red or yellow in color. In tide pools or sheltered places on the rocks is the home of the sea anemone (Fig. 3:12).

Of particular interest are the sea squirts (Fig. 39:44) which look like little leather bags attached to the rocks and in many cases are scarcely distinguishable from the general background. These animals are chordates and have a free-swimming larval stage built on somewhat the same plan as the vertebrates, revealing thereby a relationship which one would scarcely expect from the appearance of the adult.

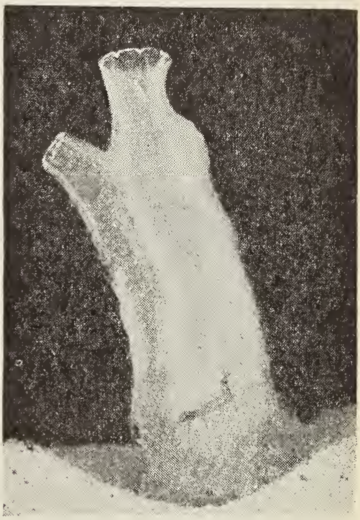


Fig. 39:44 A sea squirt (*Ciona*, phylum Chordata, subphylum Urochordata), an humble and sedentary relative of the vertebrates. Photograph by J. W. Mavor.

Hidden among the rocks and seaweed, ready to side-step out on the approach of anything they can lay their claws on, are the rock crab and the Jonah crab. They are not particular about their food, eating anything they can obtain, dead or alive, plant or animal. Crabs (Fig. 39:51) are near relatives of lobsters, the chief difference being in the shape and proportions of the body. The body of a lobster is divided into two distinct portions of about equal length. The front or anterior portion is the cephalothorax, the posterior portion the abdomen. The abdomen contains large muscles and provides most of the edible material. In a crab the cephalothorax is flat, rounded, and forms the greater part of the animal, the abdomen being represented only by a small triangular structure on the under side at the posterior end. Scarcely ½ inch long, darting to and fro among the algae, now on one side of their bodies, now on the other, are the little water fleas, not fleas at all but crustaceans of a primitive type.

(2) A SANDY BEACH

A quite different scene presents itself on an exposed sandy beach (Fig. 39:45). Near the high-tide mark extends a line of dead seaweed and other debris washed up by the waves. Upon this decaying mass various insects feed and especially the little beach flea which lives in burrows in the sand. It is a near relative of the water flea and, like it, a primitive crustacean. Nearer to the water may be seen little oval lumps in the sand which on inspection are found to contain sand-collar snails (Fig. 39:46), so named because they lay their eggs in a collar made by cementing together grains of sand. This sea snail, like some of those already mentioned, feeds on bivalves, drilling holes in their shells. Near shore small transparent shrimps may be seen swimming not far below the surface.

Fig. 39:45 Sandy beach, Woods Hole, Mass. Photograph by J. W. Mavor.

Crawling along in shallow water, pushing the sand ahead of him comes the king crab or horseshoe crab (Fig. 39:47). He appears to consist of a gigantic head with ancient-looking eyes and a long pointed tail which he often holds straight up in the water. A second look will show that what appears to be the head is hinged about the middle and consists of an anterior horseshoe-shaped portion, which is really head and thorax combined, and a posterior triangular part which is the abdomen. He is quite harmless in spite of his looks, so lift him up and turn him over. You will find six pairs of elongated appendages attached to the cephalothorax and surrounding the mouth. The first five pairs have little pincers on their ends and are used in getting food. The sixth pair is used by the animal in pushing itself through the sand. The abdomen also has six pairs of appendages but they are not used as legs. The first pair forms a broad plate which covers the remaining five. These bear the gills which are in the form of numerous thin sheets. Horseshoe crabs live on marine worms and other small animals. They come to sandy beaches in the summer to lay their eggs. The young horseshoe crab as it emerges from the egg resembles a trilobite (Fig. 40:4), a type of arthropod which flourished in the early Paleozoic era and became extinct some two hundred million years ago. So the king crab, which is not really a crab, is truly a "living fossil."

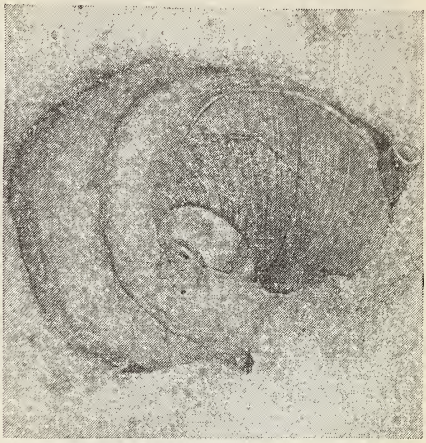


Fig. 39:46 A sand collar snail (*Natica*, phylum Mollusca, class Gastropoda) crawling along in the water with part of its foot under the sand and the siphon through which it breathes out in front (to the right). The shell is partly enclosed by the foot which, however, can be completely withdrawn and the opening in the shell closed by a horny plate, the operculum. Photograph by J. W. Mavor.

But most of the animal life on such a beach is hiding in the sand. An interesting animal common on some parts of the Atlantic seaboard is *Hippa* (Fig. 39:48). The anterior part of this little creature is not unlike that of a lobster but its abdomen is relatively smaller and is bent under the anterior portion like that of a crab. It lives on sandy beaches between tide marks and can dig into the sand with incredible rapidity using the posterior portion of the abdomen as a scoop. The lady crab sits buried in the sand with only its antennae and eyes exposed. Disturb it and if you look quickly before it disappears

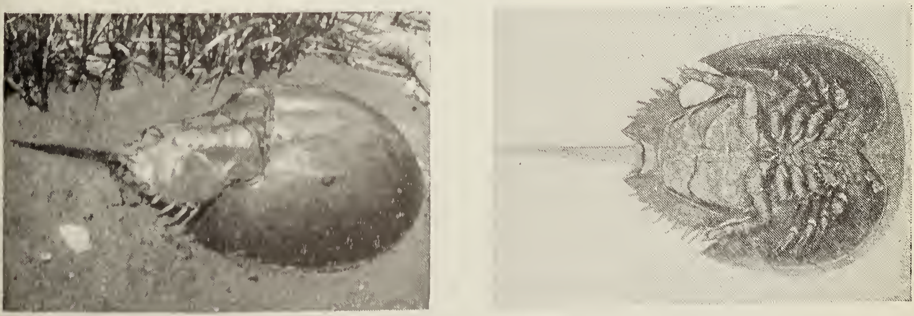


Fig. 39:47 The king crab (*Limulus*, phylum Arthropoda, class Arachnoidea). On the left an individual crawling over the sand. On the right, the underside showing the appendages. Photograph by J. W. Mavor.

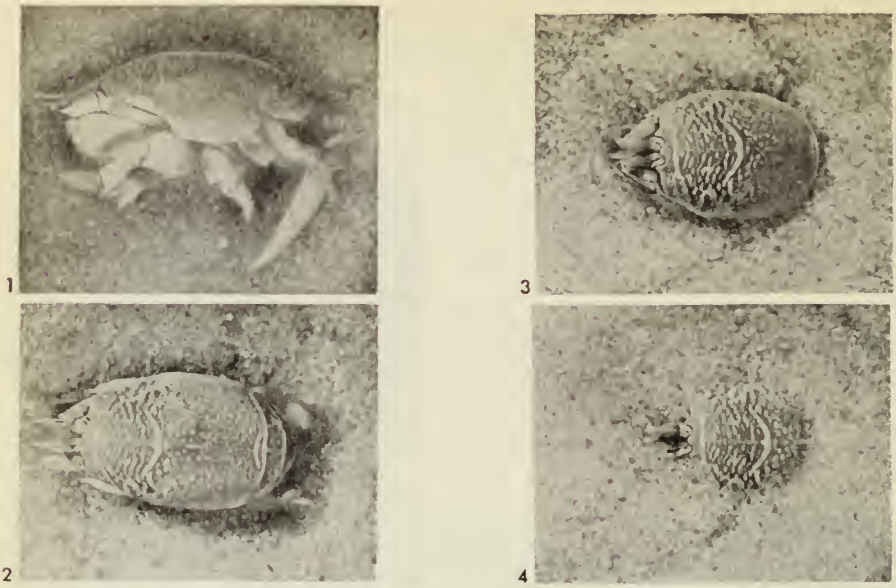


Fig. 39:48 A hippa (*Hippa*, phylum Arthropoda, class Crustacea) burying itself in the sand. In the first photograph, Number 1, the animal is on its side showing the large shovel-shaped appendage and the two smaller appendages with which it digs itself into the sand with great rapidity. The three following photographs, Numbers 2 to 4, show the animal entering the sand. Photographs by J. W. Mavor.

into the sand again you will notice that the hind legs are paddle shaped. Deep down in the sand is the razorshelled clam, so called because of the elongated razorlike shape of each of the valves of its shell.

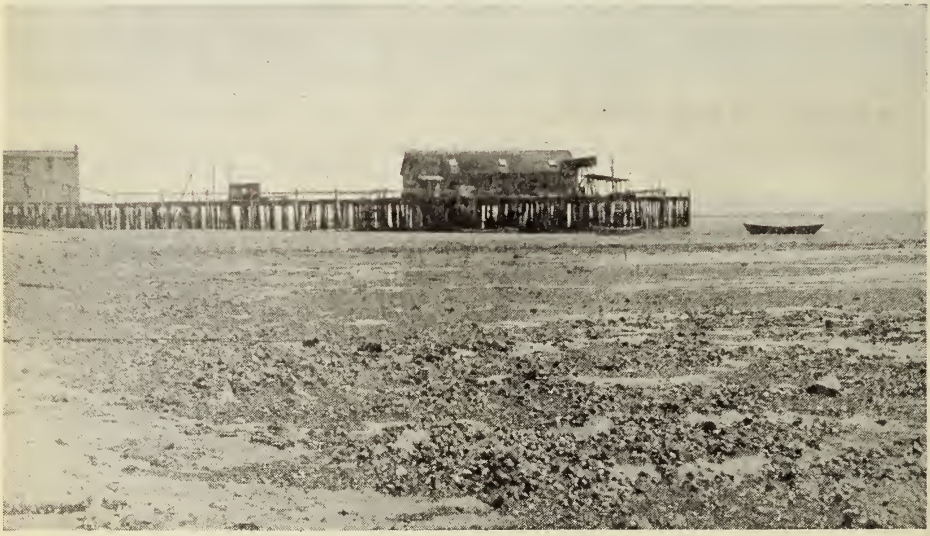


Fig. 39:49 Sand and mud flats at Provincetown, Mass. Low tide. Photograph by J. W. Mavor.

(3) SAND AND MUD FLATS

Sheltered sand and mud flats (Fig. 39:49) provide homes for all kinds of burrowing animals. Here is the home of the soft-shelled or long-necked clam (Fig. 39:50) of clam chowder and clambake fame. These animals burrow in the sand and mud sometimes to a depth of a foot, their long siphons or "necks" extending to the surface where their presence may be detected by little holes out of which water squirts on the approach of a footstep.

The blue crab (Fig. 39:51), next to the lobster our most important edible crustacean, is common on mud flats. A "soft-shelled" crab is simply one which has recently molted or cast off its hard covering or carapace and in which the new carapace has not yet become hard. Here also lives the curious spider

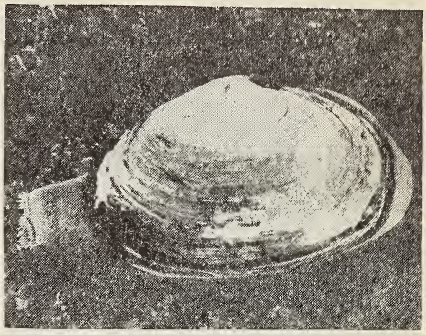


Fig. 39:50 A soft-shelled clam (*Mya*, phylum Mollusca, class Pelecypoda). The hinge of the two valves of the shell (regarded as dorsal) is above. The two siphons (which are posterior) are to the left. Water is taken in through the ventral siphon (the lower and larger of the two) and passed out through the dorsal siphon. The foot protrudes slightly from the shell to the right. When the clam is undisturbed the valves of the shell are somewhat separated and the foot and siphon protrude to a much greater extent, justifying the name "long-necked clam." Photograph by J. W. Mavor.

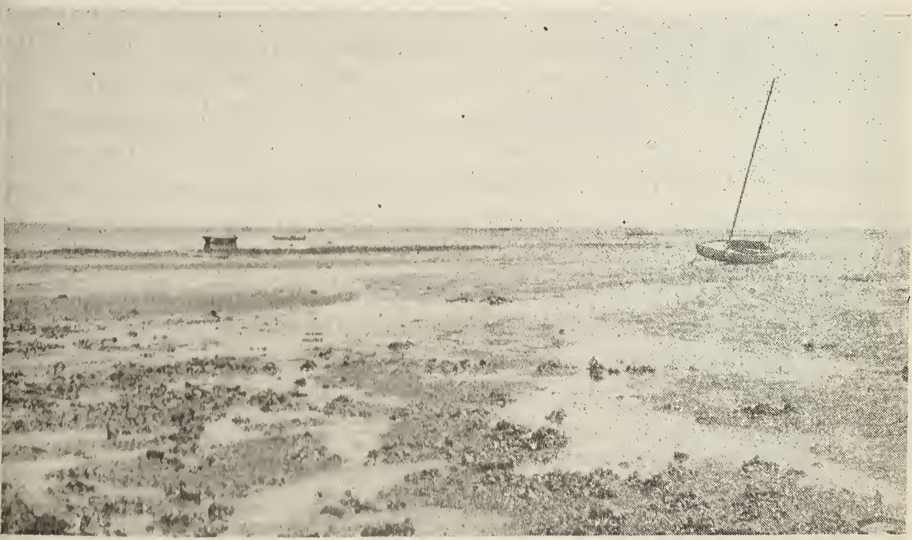


Fig. 39:49 (*Continued*)

crab, so named from its spiderlike shape, which has the remarkable habit of disguising itself by covering its carapace with seaweed. Still another interesting crab is the fiddler crab which lives in burrows that often open above high-water mark. In the male, one of the pincers, usually the right, is enormously developed at the expense of the other.

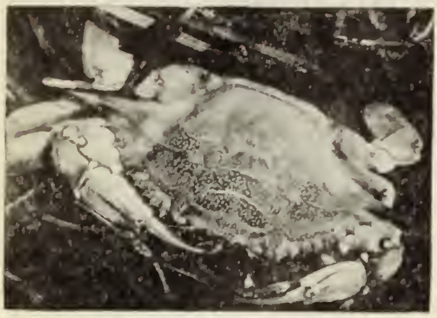


Fig. 39:51 A blue or edible crab (*Callinectes*, phylum Arthropoda, class Crustacea). Note that the last pair of walking legs are paddle-shaped for digging in the mud and sand. Photograph by Mary Dickerson, reproduced by courtesy of the American Museum of Natural History, New York.

The most characteristic animals of the sand and mud flats are the burrowing worms (Fig. 39:52) which, however, are seldom seen by the ordinary observer as they remain hidden when the sand is exposed at low tide. One of the commonest of these is the clam worm. This is a large segmented worm reaching 1 foot in length and ⅓ inch in diameter. On each segment is a pair of fleshy "legs" (parapodia). There is a distinct head which bears several pairs of tactile organs and four simple eyes. The worm is omnivorous. When feeding, the pharynx is everted, exposing two sharp teeth with which the prey is seized. Many marine worms are of great beauty. The ornate worm (Fig. 3:19) lives in a tube in the sand. Its head is surrounded by numerous long, fine filaments which serve both for respiration and for food-getting. The filaments reach out of the tube in all directions and entangle small animals. One of the most peculiar of the segmented worms is the bristle-winged worm. This worm lives in a U-shaped parchment tube. It is brilliantly luminescent over the greater part of its body. One of the segments in the middle region of the body bears a pair of large winglike structures which keep up a rhythmical movement causing the water to circulate through the parchment tube.

There are food chains on the seashore just as there are in fresh water ponds. Thus microscopic plants and animals of the seashore provide food for the bivalve mollusks such as clams, muscles, and oysters, and for barnacles. Sea weeds are browsed upon by sea urchins and gastropods such as the periwinkles. Worms and small crustacea live to a large extent on the organic debris present in the sea water, especially over mud flats. Other gastropods feed on bivalves, starfish, and barnacles. Flatfish feed on gastropods; other fish on sea anemones, worms, and crustacea. Finally, man feeds on fish, not to mention oysters and clams.

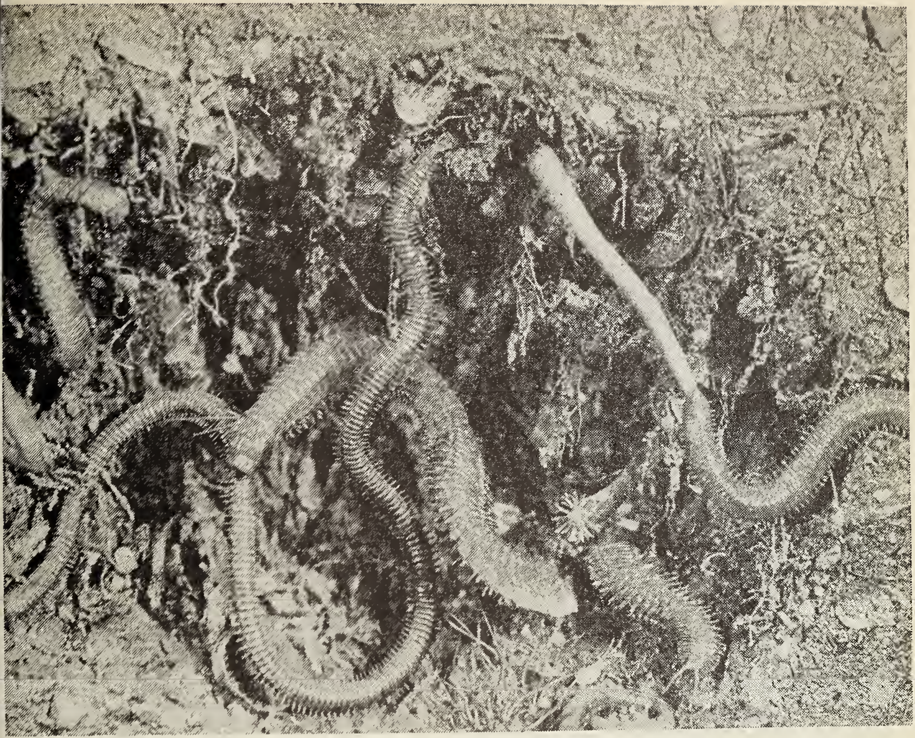


Fig. 39:52 A group of segmented bristle worms (phylum Annelida, class Chaetopoda, order Polychaeta) burrowing in the mud among the roots of eel grass. In the center a clam worm (*Nereis*) recognizable by its large segments, is attacking an opal worm (*Arabella*), the longer of the two. To the right a beak thrower (*Glycera*) seems about to enter the combat by protruding its long white proboscis ending in four teeth. Photograph of a habitat group. Reproduced by courtesy of the American Museum of Natural History, New York.

B. THE SHALLOW WATER OFF SHORE

From the tidal zone an area of shallow water extends for a varying distance out to sea. In this shallow-water zone a population as dense and varied as that of the seashore flourishes. The bottom is usually soft sand or mud mixed with rocks and shells, providing thus a suitable substratum for all kinds of organisms. Many of the shore animals already considered extend their range out into this zone, while there are many types of worms, sea snails, bivalves, crabs, sea urchins, and other animals which occur here and not in the tidal zone.

The scallop (Fig. 39:53) does not spend its life in a burrow like many bivalves but is able to swim over the sea bottom in a rather clumsy way by opening and closing its valves. A smaller species occurs on mud flats and a large species in deeper water. They are caught by dredging. The

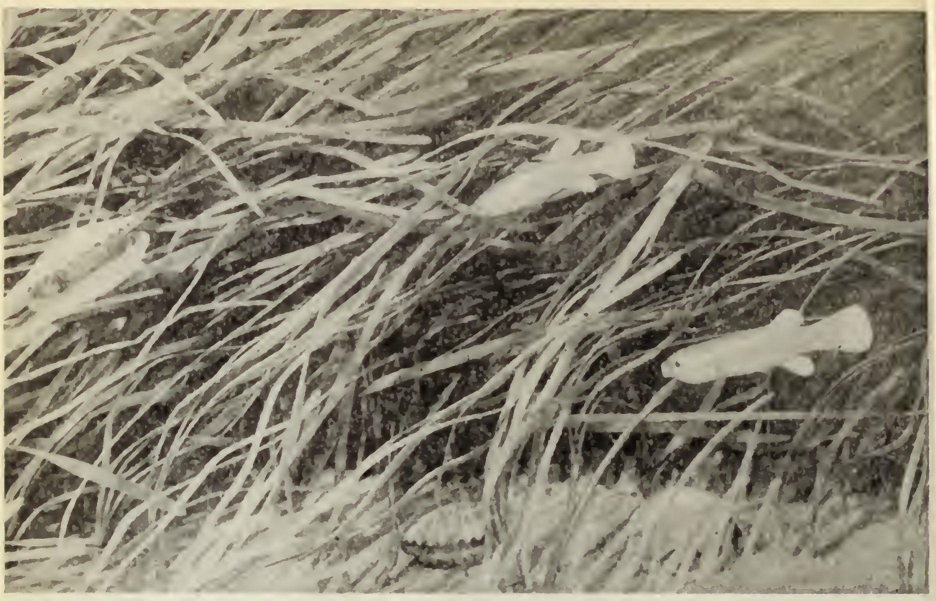


Fig. 39:53 Life in shallow water off shore. On the bottom in the center foreground and swimming on the left are scallops (*Pecton*, phylum Mollusca, class Pelecypoda). Small fishes (*Fundulus*, class Osteichthyes, subclass Actinopterygii, order Teleostei) swim through the eel grass. Photograph of a habitat group. Reproduced by courtesy of the American Museum of Natural History, New York.

part of the animal so delicious when fried is the large muscle which closes the valves. Along the edge of the tissue which lines the shell are numerous brightly colored eyes which warn it of the approach of danger. The

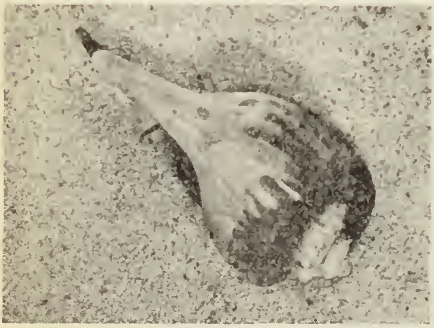


Fig. 39:54 A conch (*Busycon*, phylum Mollusca, class Gastropoda) in shallow water crawling over the sand. The siphon through which it passes water for its respiration is the dark conical structure on the extreme left. The foot and tentacles show as dark bodies under the shell. Photograph by J. W. Mavor.

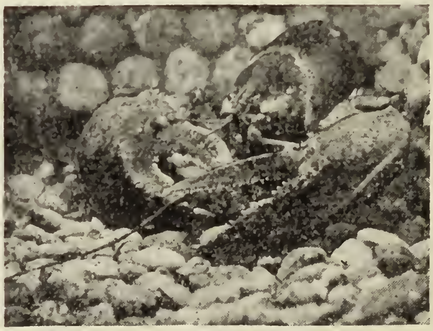


Fig. 39:55 A lobster (*Homarus americanus*, phylum Arthropoda, class Crustacea) in a characteristic pose on the lookout for food and ready for enemies. The large claws or pincers are thrust out in front. The first and second antennae extend forward and the stalked eyes cover the scene. Photograph by J. W. Mavor.

danger may be a whelk, one of the commonest of the large sea snails of the eastern coast, much used for bait by fishermen on account of its tough flesh which stays on the hook. Whelks feed on bivalves like the scallop dead or alive. Also to be found are conchs (Fig. 39:54).

The lobster (Fig. 39:55) lives in the shallow water off shore where it hides in rocky crevices or even buries itself in the sand or mud. It feeds on whatever it can obtain, seizing it with its powerful claws. The eggs are carried about by the female on the abdominal appendages until they hatch into free-swimming larvae very much like the adult. The common prawn shrimp is a swimming animal which somewhat resembles a lobster.

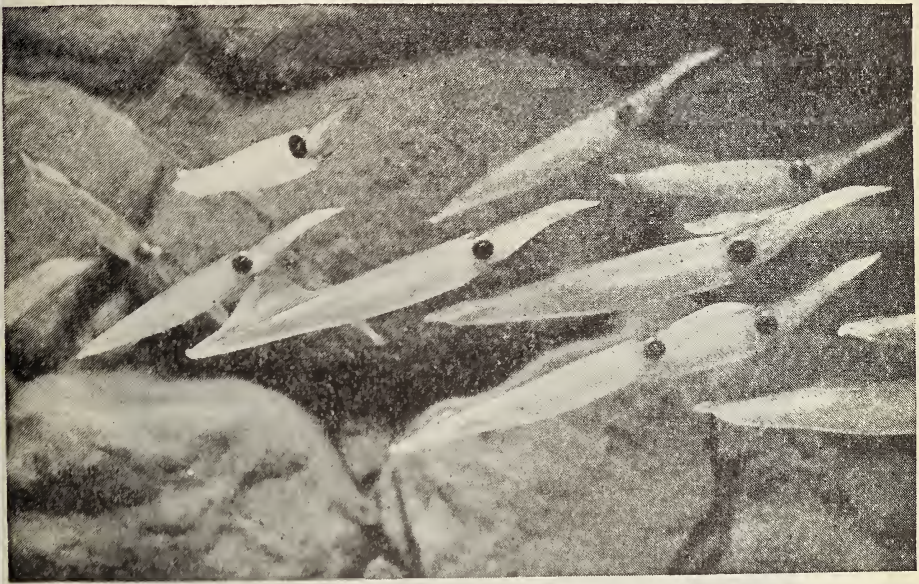


Fig. 39:56 Squids (*Loligo*, phylum Mollusca, class Cephalopoda). The tentacles are held together in front forming a conical snoutlike projection. The large black eyes and lateral fins can be seen. Photograph by J. W. Mavor.

Squids (Fig. 39:56) are graceful swimmers with beautiful iridescent bodies which are forever changing color. They progress either forward or backward with equal ease by the undulatory movements of two lateral fins, and backward by squirting water out of a funnel-shaped organ near the anterior end of the body. Two large eyes give to the head a slightly human appearance which, however, is soon changed to that of a monster when the ten writhing arms separate and feel for prey. Squid swim in shoals and feed on fish. The octopus, also a mollusk, resembles the squid but is a bottom dweller with a rounded body and eight arms. It feeds on fish and crabs, crawling out from its hiding place in the rocks and catching them with its long arms.

The dominant denizens of the sea over the shallow-water area are the fishes. Some of these are bottom forms feeding on the abundant life which covers the floor of the sea, while others spend their lives swimming near the surface or deeper down feeding on other smaller swimming creatures. The herring is a typical free-swimming fish, moving near the surface in great shoals and feeding on small crustacea. Similar in habits and related to the herring is the mackerel. To the bottom forms belong the flatfish such as the flounder, sole, plaice, and halibut. They are flattened from side to side and lie on the bottom on one side which is usually white, while the other side changes color to match the surroundings. When it hatches from the egg the young fish is like any other small fish, but as it grows older its body becomes flattened and the eye which would face the sea bottom moves over to the other side of the head so that both eyes come to be on the upper side of the fish. Flounders feed chiefly upon worms and mollusks which they scrape up from the bottom or even dig from the mud. The angler fish is flattened in the other direction, i.e., up and down. He is a poor swimmer and sits upon the sea bottom dangling his bait, which consists of a little knob of his own flesh on the end of a long rodlike

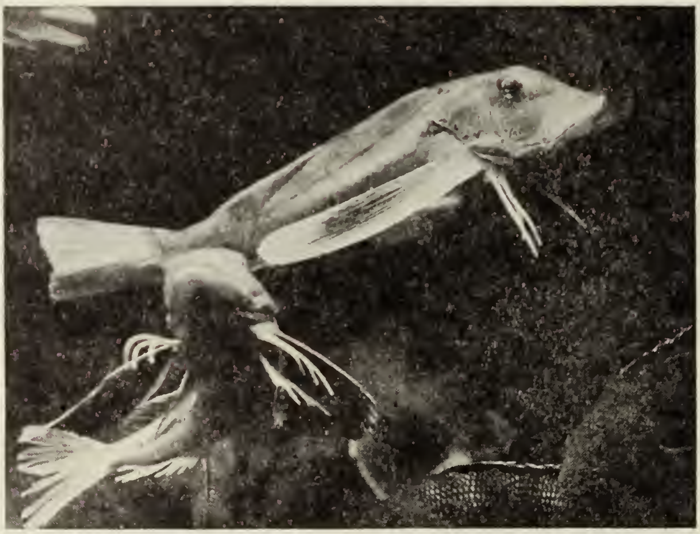


Fig. 39:57 Sea robins and sea bass (both class Osteichthyes, subclass Actinopterygii, order Teleostei). In the sea robin (*Prionotus*) the pectoral fins take the form of long fingerlike processes with which the fish crawls over the sea bottom. Its large mouth and powerful jaws are well suited to its diet of marine worms and mollusks. The sea bass (*Centropristes*) are at the lower right. Photograph by J. W. Mavor.

spine, in front of his large mouth. Another curious bottom fish is the sea robin (Fig. 39:57) which crawls along on modified spinelike fins.

Our most important food fishes live in the waters covering the various ocean banks, such as the Newfoundland Banks, the Georges Banks off the coast of Maine, and the Dogger Banks in the North Sea. It is to these banks that the fishing schooners and trawlers go from Nova Scotia, from Gloucester, and other New England fishing ports and from the coasts of England and France.

C. LIFE IN THE OPEN OCEAN

Life in the open ocean, like life on land, in fresh water, and on the sea shore, is dependent ultimately on plants. In the open ocean these plants are chiefly microscopic algae of the kind known as "diatoms." These flourish near the surface and grow only within the depth to which light penetrates. Diatoms form a very important and considerable proportion of the plant life of the ocean. Being green plants they manufacture their food materials from inorganic substances. To a large extent they make possible the animal life, and may therefore not inappropriately

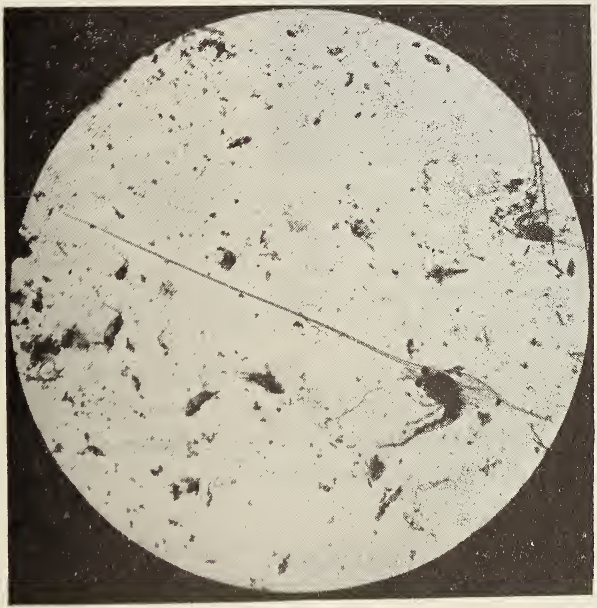


Fig. 39:58 Marine plankton from off shore. The animal which looks like a medieval knight charging an adversary in the lists is only the larva of a small crab (phylum Arthropoda, class Crustacea). The long lance which it seems to carry is an extension of its carapace and serves by increasing the surface tension to keep it near the surface. Other crustacea are scattered about the microscopic field. Photograph by J. W. Mavor.

be said to form the "pasture of the sea." Small animals, many of them also microscopic (Fig. 39:58), feed on the diatoms. All of these floating organisms show special adaptations to keep from sinking. One common adaptation is the development of long and fine processes (Fig. 39:58). The small animals are food for the larger ones. Thus the varied life of the open ocean, including many kinds of worms, mollusks, crustaceans, fishes, turtles (Fig. 39:59), sea birds, and whales, is in the ultimate analysis supported by microscopic plants. For the ocean these microscopic plants take the place of the trees, shrubs, and herbs of the forests and the grasses and herbs of the prairie. The animals and bacteria of the deep sea are dependent for their nourishment on the organisms and organic matter which gradually sinks down from the superficial layers. The life of an ocean like that of a forest, a prairie, or a pond forms a community — a community which exists on a vast scale and which moves with the great ocean currents.

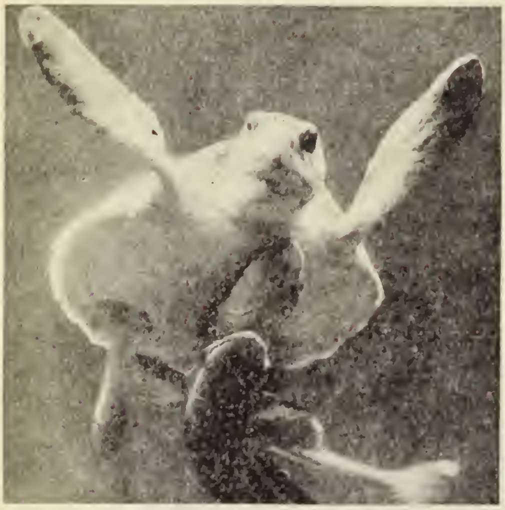


Fig. 39:59 Stealing a ride in the ocean. Two remoras or sharksuckers (*Echenis*, class Osteichthyes, subclass Actinopterygii, order Teleostei) attached by their sucking discs to the underside of a loggerhead turtle (*Carette*, class Reptilia, Order Testudinata). Photograph by J. W. Mavor.

5. GEOGRAPHICAL DISTRIBUTION

As already illustrated in the preceding sections, each species of animal or plant has its particular place or niche in the community of which it forms a part and is particularly adapted to the inorganic and organic conditions of this niche. However, a species is seldom if ever found in all apparently suitable environments. Each species is confined to a certain **geographic range** beyond which it does not naturally occur. Thus there were no rabbits in Australia before they were introduced by the European settlers. That Australia provided a suitable environment is proved by the rapid increase of the rabbit there after it was introduced. Many other similar examples could be cited.

A. CENTERS OF DISPERSAL AND BARRIERS

In most cases the distribution of the species, genera, and even larger groups of plants and animals is best explained by assuming that each has arisen at a certain point on the earth's surface, called a **center of dispersal** and has spread out to occupy the area it now inhabits. In this process of dispersal each species encounters barriers which check or prevent its further spread. **Geographic barriers** are of many types and differ with the species. Thus for a land animal or plant a river, lake, or an arm of the sea may be a barrier; for an aquatic animal or plant, land is a barrier. For animals of the plains or lowlands, a mountain range is a barrier; for an alpine plant or animal, low country may be a barrier. For animals and plants of a humid region, a desert is a barrier; for desert plants and animals, a humid region is a barrier. Similar relations exist for light and temperature. Indeed any unfavorable feature of the environment, inorganic or organic, may act as a barrier. Thus lack of food due either to the absence of certain food plants or animals from a region or due to other competing and more successful species may be a barrier. Enemies in the form of predatory animals or parasites may restrict the distribution of a species.

B. GEOGRAPHICAL REALMS

The study of the geographic distribution of plants and animals over the land areas of the earth has led to the recognition of six main realms, separated by major barriers consisting of the great oceans, inland seas, mountain ranges, and marked differences in climate (Fig. 39:60). These regions are:

Nearctic: [1] Greenland and North America as far south as Mexico.
Palearctic: All of Europe and the northern portion of Asia.
Neotropical: Central America, the West Indies, and South America.
Ethiopian: Africa and the southern portion of Arabia and Madagascar.
Oriental: The southern portion of Asia, Malay States, Sumatra, Borneo, Java, Celebes, and the Philippines.
Australian: Australia, New Zealand, Tasmania, New Guinea, and the Pacific Islands.

The animals and plants of the Nearctic and Palearctic realms do not differ so strikingly as those of the other realms and hence these realms are sometimes grouped together as a single Holarctic Realm.

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[1] The use of the term "arctic" in this connection is rather unfortunate since the realm extends southward to the Tropic of Cancer, but the term is well established.

Each of the geographic realms has a characteristic fauna and flora differing from that of the other realms. Characteristic animals of the different realms are as follows:

Nearctic: Opossum, skunk, raccoon; blue jay, turkey; rattlesnakes; mud puppy; gar pike (Lepidosteus), bowfin (Amia).

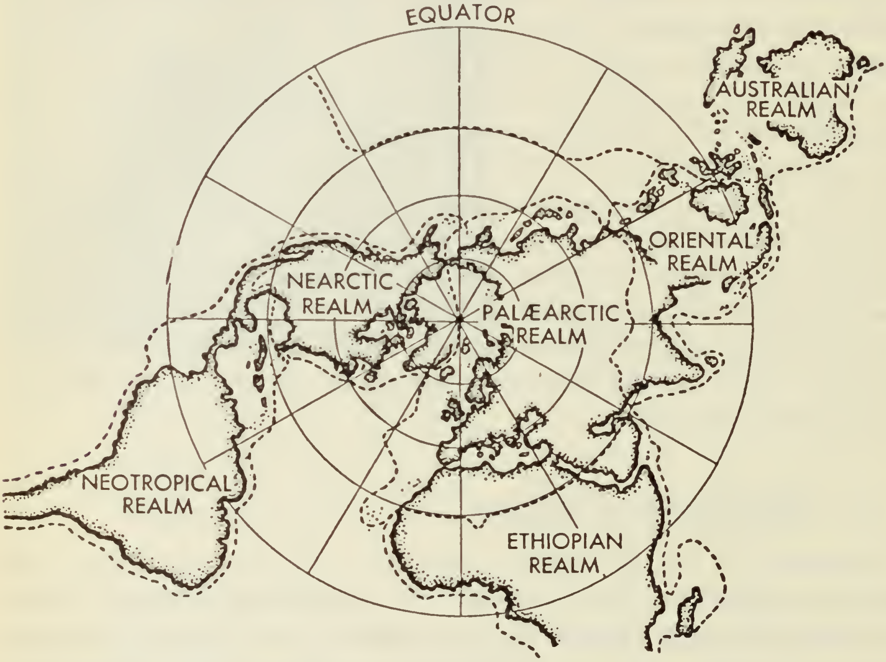

Fig. 39:60 The realms of geographical distribution of animals and plants. The dotted lines represent the boundaries of the realms. Redrawn after Lull, *Organic Evolution*, The Macmillan Company.

Palearctic: None of the larger groups or orders or even families are confined to this region, only individual species and genera are characteristic. Characteristic are moles, sheep, goats, oxen, antelopes, certain species of deer, pheasant, magpies, certain reptiles, amphibians, and fresh-water fishes.

Neotropical: New World monkeys, llamas, peccaries, sloths, armadillos, anteaters; rhea (a large ostrichlike bird), toucans, hummingbirds, many types of reptiles and fish.

Ethiopian: Gorilla, chimpanzee, several baboons, most lemurs, African elephant, hippopotamus, two or three species of rhinoceros, zebra, giraffe; secretary bird, and many other birds; many reptiles and fishes, including the lungfish, *Protopterus.*

Oriental: Orang-utang, gibbon, numerous lemurs, tiger, Indian elephant, Indian tapir, three species of rhinoceros, chevrotains or mouse deer; peacock, pheasant, jungle fowl.

Australian: The most striking feature is the total absence of *Eutheria*, the indigenous mammals being, with one exception, *Metatheria* or *Prototheria;* emu, cassowary; birds of Paradise; many reptiles, amphibians, and fishes, including three species of lungfish.

The distribution of many animals and plants has been considerably changed by human agencies, especially during the last few centuries, centuries of exploration, travel, and colonization. Thus the common house sparrow is really a European and northern Asiatic bird and was first introduced into North America in 1851. The changes in the distribution of the two common species of rats, the house rat, *Mus rattus*, and the brown or Norway rat, *Mus norvegicus*, during historic time, reflect the movements of the human race on the surface of the globe. Both species are of Asiatic origin, the house rat being native to India, the Norway rat to central Asia. The house rat is said to have been introduced into western Europe in the thirteenth century and the Norway rat, which has largely superseded it, in the eighteenth century. Both species came into North and South America with the colonists. They are now cosmopolitan, being a frequent pest in ports and on vessels. Thus in studying the geographical distribution of animals it is necessary to distinguish between **indigenous** and **introduced species.** An indigenous species is one which there is every reason to believe originated and has continued to exist in the locality. An introduced species is one which probably had its origin elsewhere and which is known to have been introduced into the area. Thus the house rat is an indigenous Indian species, but an introduced American species.

C. CLIMATIC ZONES

The geographic realms may be divided into smaller regions or zones based on climate and the dominant vegetation. A series of similar zones occurs in the Nearctic and the Palearctic realms. In the Nearctic Realm the zones include the tundra, coniferous forests, deciduous forests, grasslands, sagebrush, desert.

The **tundra** extends from the perpetual snow and ice surrounding the North Pole southward to where the coniferous forests begin. Temperatures are low and there is little sunshine except during the short summer, when only the upper layer of the soil thaws. The frozen subsoil prevents the seepage of the water from the melting ice and snow with the result that in summer many lakes, ponds, and marshes are formed. The dominant plants are mosses, lichens, grasses. The mammals include musk ox, arctic fox, and arctic hare. Many migrating water birds come here to breed. There are no reptiles; being cold blooded they are unable to survive the winter.

The **coniferous forests** extend southward from the tundra to the northern United States and further south in the mountain ranges such as the Rockies and Appalachians. The winters are cold and stormy, summers cool with moderate rainfall. The dominant plants are pines, firs, spruces, and cedars. The animals include moose, caribou, elk and deer, and many "fur animals" such as fox, lynx, marten; a number of perching birds; and a few reptiles and amphibians.

The **deciduous-forest** zone extends from the eastern states westward to the Mississippi Valley. The climate and life of a forest of this type is described in a previous section of this chapter (Art. 2, Sec. A).

The **grassland zone** comprises the prairies and the Great Plains and includes the Mississippi Valley. The climate and life of a grassland have already been described (Art. 2, Sec. B).

The **sagebrush zone** occupies most of the great plateau (Great Basin) between the Rocky Mountains and the Sierra Nevada range. Here the climate is dry, the winters cold, and the summers hot. It is a semidesert region. The dominant vegetation is sagebrush (a kind of shrub) with bunch grasses. The animal life resembles that of a desert, with burrowing animals, many reptiles.

The **desert zone** extends from southwestern Texas to southern California. It is a region of slight rainfall with hot clear days and relatively cool nights. The plant and animal life is similar to but more restricted than the life of the sagebrush zone.

In the Neotropical, Ethiopian, Oriental, and Australian realms another zone, that of the tropical rain forests, occupies large areas. This zone is absent from the Nearctic and Palearctic realms.

The **tropical-rain forest zone,** most of which is included between ten degrees on either side of the equator, has a continuous warm climate and a heavy rainfall throughout most of the year. This is the region of tropical jungles with tall, large-leaved trees and luxuriant vines. The actual plants and animals differ in the different realms and include many species of ants, anteaters, sloths, bats, monkeys, many highly colored birds, and reptiles.

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Questions

1. Go into a forest or onto a prairie and try to determine why the different plants and animals are there.
2. Most forest birds sing only when perched while most prairie birds sing on the wing. Can you think of any reasons for this?
3. Try to work out what would happen if someone went into a forest and killed (*a*) all the deer mice, (*b*) all the shrews.
4. List some adaptations of plants and animals to (*a*) life in a forest, (*b*) to life on the prairie.
5. Compare the conditions of life in a fresh-water pond with life on the seashore.
6. Remembering that life probably originated in the sea, what are some of the main differences between the plants and animals of a fresh-water pond and those of the seashore?

7. Explain the difference between the plants growing in the water along the edge of a pond and the plants in the sea along the shore.
8. Why do many of the animals found along the seashore have shells?
9. Explain the presence of the following animals in a pond: duckweed, dragonfly larvae, diving beetles, air-breathing snails, muskrats.
10. Explain the presence of the following in the ocean: whales, dolphins, turtles, penguins, eelgrass. Why are there almost no flowering plants, ferns, or mosses in the sea?

Suggestions for Further Reading

Pool, Raymond J., *Basic Course in Botany*, Ginn and Company, Boston, 1940, Chap. XVII, "Plants and Their Environment."

Weaver, J. E., and F. E. Clements, *Plant Ecology*, 2d ed., McGraw-Hill Book Company, Inc., New York, 1938. A rather technical book.

Clements, Frederic E., and Victor E. Shelford, *Bio-ecology*, John Wiley & Sons, Inc., New York, 1939. A technical textbook with emphasis on the prairie.

Needham, James G., and J. T. Lloyd, *The Life of Inland Waters*, Comstock Publishing Company, Inc., Ithaca, N. Y., 1916.

Morgan, Ann H., *Field Book of Ponds and Streams*, G. P. Putnam's Sons, New York, 1930. A useful book for anyone who wants to study ponds and streams and to know the names and life histories of the animals and plants found in them.

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CHAPTER 40

The History of Life on the Earth

1. HOW THE RECORD WAS MADE

A. HOW FOSSILS ARE FORMED

A **fossil** is the actual remains of a part or all of an organism or any impression or trace of an organism from a previous age preserved in the earth's crust (Fig. 40:1). Fossils have been formed and the preservation effected in a number of different ways.

(1) PRESERVATION OF THE ACTUAL ORGANISM

THE SOFT PARTS. Some years ago the body of a long extinct species, the mammoth, was found by a hunter in the frozen soil of northern Siberia. It had been in cold storage for some 20,000 years. The flesh was still red. In all about fifty such carcasses have been found preserved in this way. Preservation almost as remarkable is seen in remains recovered from oil containing rocks where the body of an animal has become soaked with the oil.

THE HARD PARTS. A fossil may form when the body of an aquatic animal or plant sinks to the bottom of a lake or sea, becomes covered with sediment, and eventually is included in a sedimentary rock. In such cases usually only the skeleton is preserved but often the outline of the animal is indicated by a thin layer of carbon which remains from the disintegration of the soft parts. The hard parts of a land animal drowned in a river or lake may be similarly preserved. The body of an organism may be buried by blown or shifting sand, or in the rain of ashes from a volcanic eruption, and the hard parts preserved as fossils.

(2) PETRIFACTION (PRESERVATION BY CHEMICAL CHANGE)

In the older rocks the parts preserved are usually **petrified** (L. *petra*, stone + *facere*, to make). The change may be brought about in a number of ways. Petrified bones are usually preserved by the pores becoming **filled with mineral matter,** the hard material of the bone remaining intact and unaltered. Such bones are heavy and stonelike. This is a very common method of fossilization. In another method of preservation the original substance of the hard part may be dissolved and **replaced,** often particle by particle, by mineral matter, such as silica or carbonate of lime. Wood is commonly preserved in this way and the process may be so delicate that the cell walls and other microscopic structures of the wood are preserved even after all organic matter has disappeared. Examples of this method of preservation are found in the petrified forests of Yellowstone Park. When the organic matter has been changed chemically so that only the carbon is left, the fossil is said to be **carbonized.** Coal consists chiefly of carbonized fossil plants. The original tissues are often beautifully preserved. In the trees of some coal beds the annual rings show so clearly that it is possible to determine that the climate of the time was uniform with little seasonal change. The arrangement and number of the stomata on the leaves can also be observed and indicates that the climate was humid.

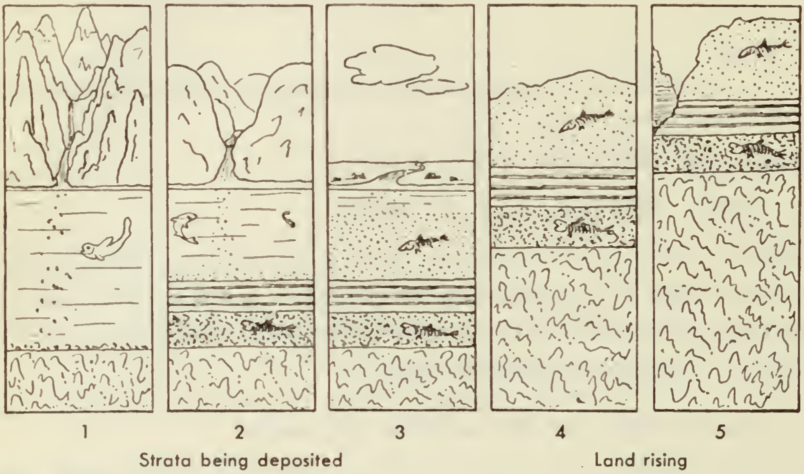

Fig. 40:1 How fossils are formed.

(3) MOLDS AND CASTS

In this case the actual organic material has been dissolved away and a mold or cavity left in the rock. The mold may then be filled with material which makes a rocky cast inside the mold. In very rare cases, casts of soft-bodied animals such as jellyfish and worms have been preserved. Some of the most remarkable molds are those of insects preserved in amber. **Amber** is the dried and hardened resin of ancient conifers.

The insects became imbedded in the resin when it was soft. Later the resin hardened and a natural microscopic preparation was made twenty-five million years ago. The insect fossils are but delicate hollow molds, the organic matter having disappeared. If the amber is dissolved nothing remains.

(4) FOOTPRINTS AND TRAILS

Fossil footprints are formed when an animal walks over soft mud or fine wet sand which afterward becomes covered with sediment and hardened. The dinosaur footprints of the Connecticut River Valley were preserved in this way.

B. CONDITIONS FAVORING FOSSILIZATION

"The Buffalo carcasses strewn over the plains in uncounted millions a generation ago have left hardly a present trace. The flesh was devoured by wolves or vultures within hours or days after death, and even the skeletons have now largely disappeared, the bones dissolving and crumbling away under the attack of the weather."[1] Only rarely and under special conditions does an animal or plant leave fossil remains. Two conditions especially favor preservation: the **possession of hard parts** and **immediate burial**. A dead animal or plant left exposed soon decays and even the hard parts dissolve and crumble away. If it is buried decay is retarded and weathering prevented. Some remarkable fossil deposits have resulted from animals being **mired** in asphalt pools, peat bogs, or quicksands. Rains of **volcanic ash** have been responsible for many fine fossil deposits. **Wind-blown sands** may overwhelm the living or bury the dead. But dry sand does not provide good conditions for preservation and fossils are rare in desert deposits. **Water-borne sediments** provide by far the commonest means of burial. Flooded streams drown and bury their victims in the shifting channel sands or in the muds of the flood plain. The sea floor near shore is usually covered with a loose shifting sediment. Here marine animals become quickly buried. The shallow water of the seashore with its abundant and varied life has provided the greatest number of fossils.

C. THE CHANCE OF A FOSSIL OCCURRING

From the previous discussion it must have become evident that although there are a number of ways in which a fossil record may occur, the actual chance of any organism or even of any species of organism leaving a fossil record is slight. Still less, however, are the chances of that record being found by man. Only where rocks come to the surface through the wearing away of the rocks above or where a river has cut a deep gorge or in the rare cases where man has dug into the crust of the earth in mines or quarries, are sedimentary rocks available for the fossil hunter. The record which fossils give us of life in the past is therefore a very incomplete one. It has, however, one great advantage over written history. Fossils are actual material things which can have been changed only by physical and chemical forces, while written history is always colored and often falsified by the allegiance or prejudice of the writer.

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[1] Schuchert, C., and C. O. Dunbar, *A Textbook of Geology*, Part II: *Historical Geology*, John Wiley & Sons, Inc., New York, 1933.

D. THE FORMATION OF SEDIMENTARY ROCKS

Everybody has seen how rocks are worn away or **eroded,** by the action of wind, rain, snow, and frost and how from the crumbled fragments soil is formed. Familiar also is the work of streams and rivers in carrying this soil from the land to deposit it in lakes or in the sea, or in times of flood over the adjoining land. The ceaseless pounding of the waves on a rocky shore gradually reduces the rocks, first to boulders, then pebbles, and finally to fine sand and mud. Material from the seashore is deposited on the sea floor, the coarser material near shore, the finer material farther out. Sediments deposited in either fresh or salt water become, in the course of time, **sedimentary rocks.**

Slow and gradual changes in level between the land and the sea have been proved to be in process at various places on the surface of the earth. Such changes in level are most easily seen and determined on the seashore. In some places, as on the eastern coast of the United States, the land is very gradually sinking into the sea, while elsewhere, as on the Pacific coast, the land is gradually rising. The sinking of the land is called **submergence.** During geological time large areas of the North American continent have at different times been submerged. Such submerged areas formed large gulfs and inland seas and became in time covered with marine deposits, in which coarse sand and pebbles mark the ancient seashore. When later an **emergence** of this land out of the sea occurs, the sedimentary rocks tell the story of the submergence.

Emergence of the land may be accompanied by a folding of the layers, or strata, of sedimentary rock and erosion of the exposed surface. The sedimentary rocks wear away unevenly, making a new landscape. When later another submergence occurs and a new layer of sedimentary rocks is formed they are deposited on the eroded surface of the older rocks and what is called an **unconformity** exists between the two layers or strata. An unconformity in sedimentary rocks indicates an unknown interval of time, usually of great extent, between the formation of the rocks which it separates.

Water is not the only agency which transports materials and brings about the formation of sedimentary rocks. During volcanic eruptions large quantities of fine ash are thrown into the atmosphere and carried by air currents to be laid as a fine dust over the land and sea. Winds pick up desert sand and transport it from place to place.

2. PIECING THE RECORD TOGETHER

A. LAW OF SUPERPOSITION

A river gorge or canyon (Fig. 40:2) often affords a good opportunity to study sedimentary rocks cut in sections. They then appear in layers or **strata,** superimposed one upon another like the layers of a cake. The different strata, and if the gorge is a deep one there will usually be several, are distinguished by the nature of the sedimentary rocks which compose

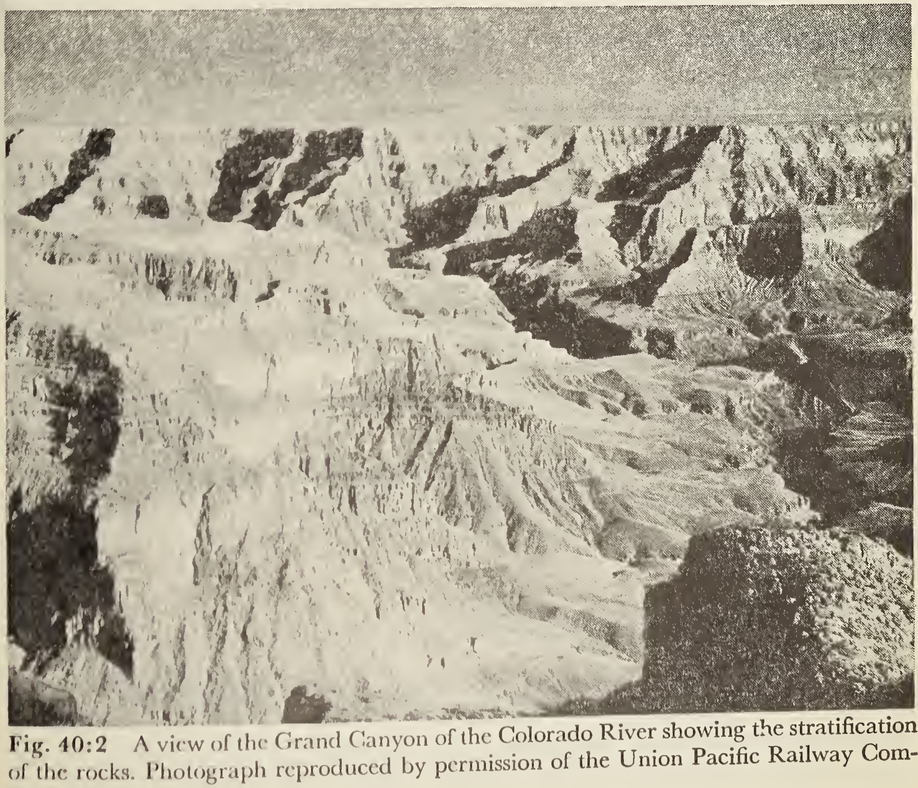

Fig. 40:2 A view of the Grand Canyon of the Colorado River showing the stratification of the rocks. Photograph reproduced by permission of the Union Pacific Railway Company.

them, i.e., whether sandstone, shale, or other rock. From our knowledge of the manner in which these rocks were formed it is clear that, in general, the strata are arranged in the order of their ages, the youngest on top, the oldest below. This simple and self-evident principle is called the **law of superposition.**

B. *IDENTIFICATION OF STRATA*

Extensive studies have been made of the fossils which occur in the strata exposed at different points on the surface of the earth. It is now well established that **each continuous layer or stratum has a characteristic group or list of fossil species** which make up its fossil fauna and flora. Some of the species may extend through several strata but most of them will be limited to a stratum formed by the continuous deposit of one type of sediment. This fact was discovered in 1798 by William Smith, a surveyor. For years Smith collected fossils from the different kinds of rocks exposed in quarries in the south of England. One day as he was cataloguing his collection he discovered that certain fossils always occurred in the same kind of rock or, as he expressed it, in the same stratum and not in other strata. He reasoned from this that fossils could be used to identify a stratum in different quarries. This method of identifying deposits by the fossils which they contain has been checked in many cases where, as in the south of England, many strata lie one on top of the other and the law of superposition can be applied. The discovery is now regarded as a fundamental principle of the science of geology.

The principle by which sedimentary rocks are classified by the characteristic groups of fossils which they contain makes it possible to correlate strata found in widely different parts of the earth and to construct a geological timetable. It should be emphasized that the application of this principle in no way assumes the evolution of organisms from lower to higher forms, that it was discovered quite independently of the idea of evolution, and that it could be applied without any consideration of evolution.

3. THE GEOLOGICAL TIMETABLE

From the foregoing it must have become evident that the rocks of the earth's crust, especially the sedimentary rocks, contain the history of the changes which have occurred on its surface. At no one place on the land is there a complete series of sedimentary rocks. Just because it is land this is impossible. The complete story must be obtained by comparing the records available in different localities and correlating them. In this way it is possible to construct a geological timetable.

The time of which we have a record in the sedimentary rocks is divided into five **eras** which are named according to the kind of living things known or inferred to exist during the era. The first or oldest era is called the **Archeozoic,** or era of primitive life, the second, the **Proterozoic,** or era of early life, the third the **Paleozoic,** or era of ancient life, the fourth the **Mesozoic,** or era of medieval or middle life, and the fifth and to date the last, the **Cenozoic** or era of modern life. The eras are divided into **periods** (Table 40:1). The rocks formed during an era make up a **group,** those formed during a period make up a **system.** Thus there is a Paleozoic group and a Cambrian system.

Recently a method using data of an entirely different kind has been found to check the results of the geologist. This method also makes possible a determination of the approximate dates (in millions of years) of the beginning and end of each era.

The element uranium changes by a long series of transformations into the element lead. When uranium and lead occur together in a small fragment of sedimentary rock otherwise free from lead and uranium it may be assumed that the lead was formed by transformation from the uranium. The rate at which uranium forms lead is independent of the conditions under which it occurs and has been determined to be such that 7,400,000,000 grams uranium yield 1 gram lead per year. Hence the age of a piece of rock containing uranium and lead can be determined from the proportions of these elements which it contains, thus:

$$\text{Age of rock} = \frac{\text{weight of lead}}{\text{weight of uranium}} \times 7400 \text{ million years}$$

The figures in the second column of the accompanying table were obtained in this way.

It may be said that throughout the period of the earth's history represented in the table the climate and other conditions were not radically different from those of recent times and were favorable to the existence of life.

4. THE FOSSIL RECORD

A. THE ARCHEOZOIC AND PROTEROZOIC ERAS

With the possible exception of one or two doubtful cases no fossils have been found in Archeozoic rocks. In rocks of the Proterozoic era fossils

TABLE 40:1. GEOLOGICAL TIMETABLE[1]

ERAS		*	PERIODS	EPOCHS	GEOLOGICAL FEATURES	FORMS OF LIFE
Cenozoic 3%	1% +		Quaternary	Recent		Dominance of man
		1		Pleistocene	Periodic glaciations	Extinction of large mammals
	2%		Tertiary	Pliocene	Large continental areas, mountains forming, including the Alps and Himalayas. Climate warm in the beginning of the period, gradually cooling	First men
				Miocene		Culmination of mammals and land floras
				Oligocene		Extinction of archaic mammals; rise of anthropoids
		60		Eocene		Spread of modern mammals. Rise of grasses
Mesozoic 7%	Late Mesozoic 4%		Cretaceous		Great swamps, followed by formation of Rocky Mountains and Andes and cooler climate	Rise of archaic mammals and birds. Extinction of dinosaurs, pterodactyls, and toothed birds. Spread of modern insects and flowering plants
	Early Mesozoic 3%		Jurassic		Great areas of lowlands near sea	Spread of primitive mammals, rise of toothed birds, spread of pterodactyls. Gymnosperms
		200	Triassic		Great desert areas	Rise of dinosaurs, pterodactyls, and primitive mammals. Spread of cycads and conifers

* Approximate time which has elapsed in millions of years.

[1] Compiled from Charles Schuchert and Carl O. Dunbar, *A Textbook of Geology*, Part II: *Historical Geology*, John Wiley & Sons, Inc., New York, 1933; and Alfred S. Romer, *Man and the Vertebrates*, the University of Chicago Press, Chicago, 1941.

TABLE 40:1. GEOLOGICAL TIMETABLE (*Continued*)

ERAS		*	PERIODS	GEOLOGICAL FEATURES	FORMS OF LIFE
Paleozoic 17%	Late Paleozoic 6%		Permian	Mountain building	Spread of amphibians and primitive insects. Extinction of trilobites and Paleozoic corals
			Pennsylvanian	Mountain building, warm, humid climate	Spread of reptiles. Extensive forests of gigantic ferns, horsetails, and club mosses
			Mississippian	Lowlands, great inland seas	Spread of ancient sharks and culmination of crinoids
	Middle Paleozoic 3%		Devonian	Inland seas followed by gradual emergence of land. Dry climate in eastern N. America and western Europe	Rise of fishes and amphibians. First spread of forests
			Silurian	Great inland seas, warm, mild climate	Rise of primitive fishes (ostracoderms). Sea-scorpions (eurypterids). First land plants
	Early Paleozoic 8%		Ordovician	Great submergence of land. Mild climate extending into arctic regions	First primitive fishes (ostracoderms). Culmination of trilobites. Spread of mollusks
		540	Cambrian	Lowlands and inland seas, probably mild climate	Dominance of trilobites. Rise of mollusks. Brachiopods
73%	Proterozoic Era			Evidence of an early and a late glacial period	Sponges, Protozoa (Radiolaria). Algae
	Archeozoic Era	2000		Geological history very obscure	Evidence of the existence of life but no recognizable fossils

* Approximate time which has elapsed in millions of years.

have been found which are said to be the remains of algae which surrounded themselves with a precipitate of calcium carbonate. Algae of this nature are common reef-forming organisms today. In these rocks are also the remains of Radiolaria and four orders of sponges. The highest type of life represented is that of wormlike creatures recorded by trails and burrows. To this short list of definite fossils should probably be added the carbon which occurs in black shales and slates and the graphite (also carbon) which occurs in beds interspersed between sedimentary rocks. Whenever, in later rocks, carbon occurs either in beds as in the case of coal, or disseminated through the rock as in that of black shales, its presence can be traced with certainty from microscopic or other evidence to the previous presence of plant or animal tissues which were buried with the sediments forming the rocks.

When it is remembered that the Archeozoic and Proterozoic eras represent together probably at least two-thirds of the time during which conditions on the earth were likely to have been suited to the existence of life, the geological record seems meager in the extreme. Two reasons may be advanced why this record may only very incompletely represent the organic population of these remote eras: The plants and animals may have been mostly soft bodied and without skeletons or other hard parts which could form fossils; we know that in many cases the rocks of these eras bear evidence of exposure to great pressures and high temperatures after they were buried beneath the rocks of subsequent eras — pressures and temperatures which may have obliterated fossil remains.

The geological evidence indicates that a long interval of time must have passed between the end of the Proterozoic and the beginning of the Paleozoic eras. Of what happened during this time except the erosion of land surfaces no record has yet been found.

B. THE PALEOZOIC ERA

For the purpose of description the Paleozoic era will be divided into Early, Middle, and Late Paleozoic. The Early Paleozoic includes the Cambrian and Ordovician periods, the Middle Paleozoic the Silurian and Devonian periods, and the Later Paleozoic the Mississippi, Pennsylvanian, and Permian periods, often called collectively the **Carboniferous.**

(1) THE EARLY PALEOZOIC

The rocks formed during the Early Paleozoic in North America were in most cases deposited in the shallow water of vast inland seas during a gradual submergence of the land, which ended with fully half of the interior of the continent under salt water. For the first time in the geological record fossils are numerous and well preserved. From the dim past life bursts upon the scene in great variety. Most of the phyla of the animal kingdom already have made their appearance. "The dominant creatures of the Early Paleozoic seas were the **trilobites,** swimming, groveling crustaceans of predacious and scavenging habits, which became so numerous and varied as to make up fully 60 per cent of the known fauna."[1] "In their day they boasted the greatest size if not the highest intelligence of any animals upon the earth. Even so, they were small, generally ranging between one and three or four inches in length."[1] The largest was about 18 inches long. It is an interesting commentary on the history of life upon the earth that these small arthropods dominated the inhabited world for a period more than one hundred times as long as that which has seen the dominance of man. Next to the trilobites in abundance came the **brachiopods,** mollusklike, shelled creatures of small size which constituted 30 per cent of the fauna. Abundant also are fossils of a reef-building form believed to represent a primitive coral and later fossils of true corals. Some remarkably well-preserved fossils from the mountains of British Columbia show many species of crustacea and worms in such fine detail that delicate microscopic hairs and the outlines of internal organs can be seen.

Among the most interesting of the fossils found in the later rocks (Ordovician) of the Early Paleozoic are fragments of bony plates which have been identified as the armor of small, fishlike creatures called **Ostracoderms.** No fossils of either land plants or land animals have been found in Early Paleozoic rocks.

(2) THE MIDDLE PALEOZOIC

Included in the Middle Paleozoic are the Silurian (Fig. 40:3) and he Devonian periods (Fig. 40:4). During this time there occurred a gradual emergence of the land from the vast seas which spread over the continent during the Early Paleozoic, so that by the end of the Middle Paleozoic the entire continent was above water.

The first unquestionable records of land plants come from rocks of the Middle Paleozoic. The earliest of these fossils represent fernlike plants, but they are rare and the structure of the plants they represent somewhat problematical. The first abundant and well-preserved fossils of land plants represent gymnosperms. In the Catskill Mountains a forest of these strange plants is preserved, tall slender trees with scalelike leaves, and bearing seeds at the ends of modified leaflets.

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[1] Schuchert, Charles, and Carl O. Dunbar, *A Textbook of Geology*, Part II — *Historical Geology*, John Wiley and Sons, Inc., New York, 1933.

But the Middle Paleozoic and especially the Devonian is best known for its **fossil fish** (Fig. 40:5). These were chiefly of two kinds, sharks (Elasmobranchii) and lungfishes (Dipnoi), the latter being provided with an air bladder which could be used as a lung. All were simple types with cartilaginous skeletons. In some respects they were more like what we would expect the ancestors of the higher vertebrates to be than are the modern fishes. Certain of the lungfishes reached a length of 20 to 25 feet and were probably the most formidable animals of the time.

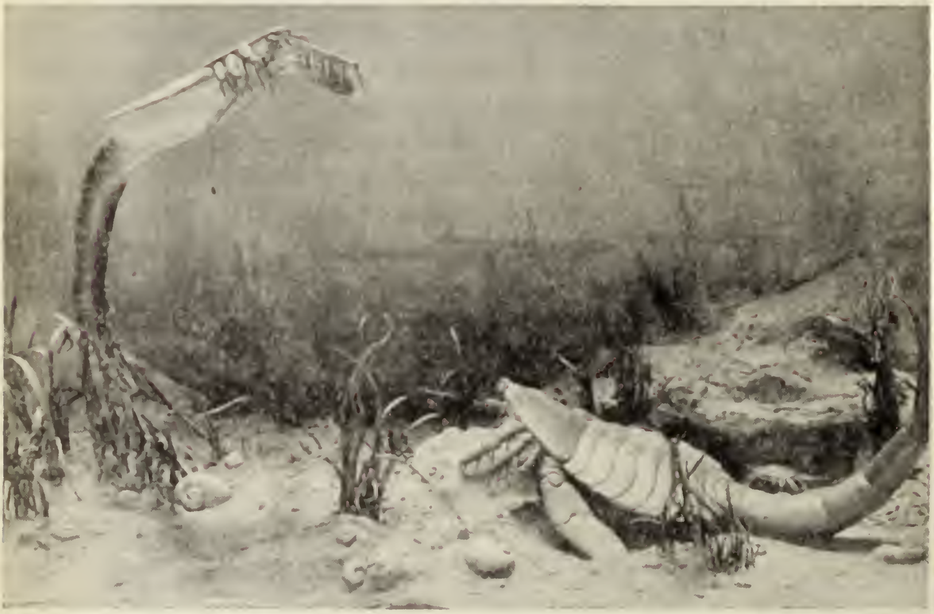

Fig. 40:3 Silurian (Middle Paleozoic) marine life from the rocks of New York State. Two large eurypterids, scorpionlike arthropods, are very much in evidence, one standing up on the left, the other approaching it on the bottom from the right. Also present on the ocean floor are the coiled shells of gastropod mollusks and algae. Photograph of a reconstruction in the New York State Museum at Albany.

In rocks deposited toward the end of the Middle Paleozoic (Late Devonian) have been found the earliest records of land vertebrates. These animals, called **stegocephalians,** were primitive amphibians. Recently several fossil skulls and limbs have been found in the Late Devonian rocks of east Greenland. The animals were not of large size compared with some of the fishes then existent, although they would be giants if placed among the amphibians of today. The skulls measured from 4½ to 7 inches in length. Our earliest records of land plants and

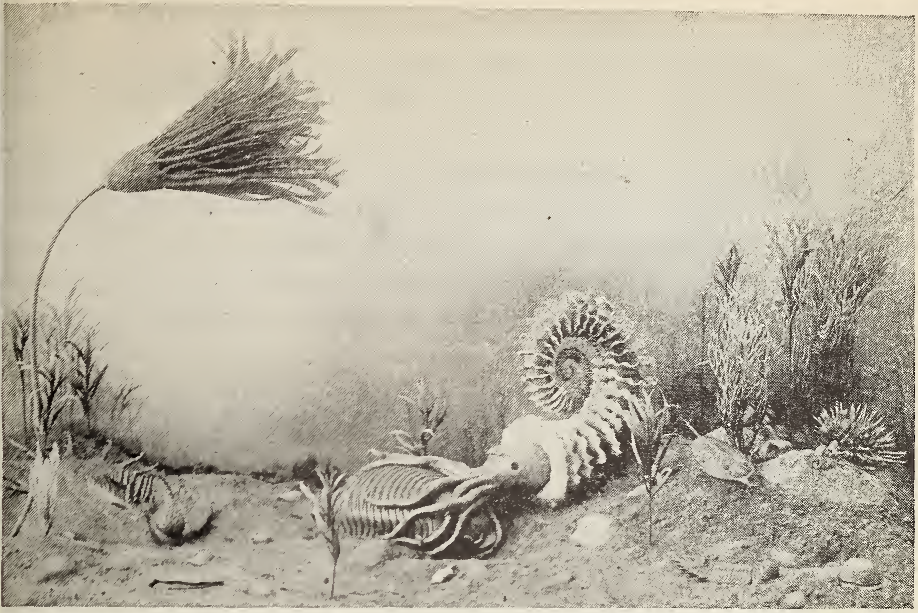

Fig. 40:4 Early Devonian (Middle Paleozoic) marine life from New York State. On the left is a large crinoid (phylum Echinodermata). The body of the animal is pear-shaped and attached by a long stalk to the ocean floor; the arms are attached to the broader end and float toward the right. Surrounding the stalk of the crinoid are algae. In front of these and partly buried in the sand is a trilobite (phylum Arthropoda) with a double row of dorsal spines. In the foreground near the trilobite several small brachiopods are on the sand. The large coiled shell with ornate flanges is that of a cephalopod (phylum Mollusca) which is attacking a trilobite. Still other trilobites appear further to the right and near the right margin is the spiny shell of a gastropod mollusk. Photograph of a reconstruction in New York State Museum at Albany.

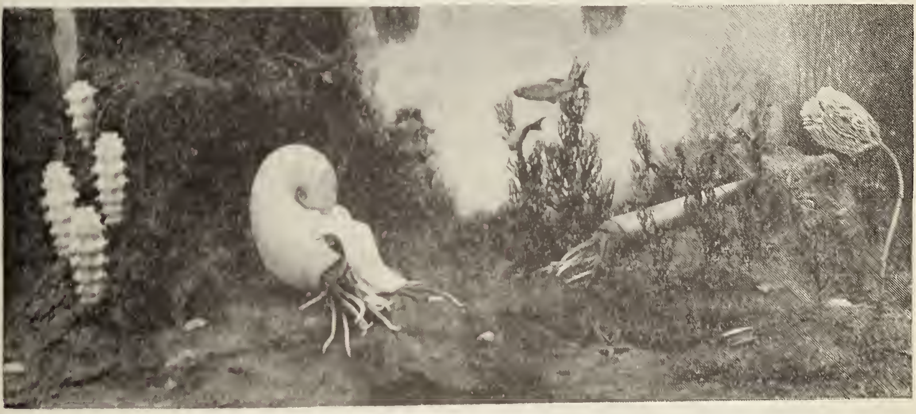

Fig. 40:5 Late Devonian (Middle Paleozoic) marine life from New York State. On the left are four beautiful vaselike glass sponges (phylum Porifera). Toward the center from them is a large cephalopod (phylum Mollusca) in a coiled shell. In the center swimming among algae are two small fishes. Lying on the ocean floor is another cephalopod which has a long, straight, conical shell. In the foreground further to the right is a starfish. On the extreme right is a crinoid. Photograph of a reconstruction in the New York State Museum at Albany.

animals come from a time when the vast inland seas of the Early Paleozoic were gradually drying up due to the emergence of the continent.

An abundant and varied invertebrate fauna existed during the Middle Paleozoic. Trilobites were decreasing. **Eurypterids** or sea scorpions, arachnids which resembled true scorpions, culminated and declined. Fragmentary fossils of one of these creatures from the Silurian of western New York indicate an animal 9 feet in length — possibly the largest arthropod which has ever existed.

(3) THE LATE PALEOZOIC

The Late Paleozoic includes the Mississippian, Pennsylvanian, and Permian periods. During this time a submergence of the southern and central portion of the North American continent was followed by an emergence in which the coast line extended even beyond its previous contour.

The great coal beds which are the most conspicuous feature of this time represent in most cases ancient peat bogs which became submerged and covered with sedimentary rocks. Usually the vegetable matter has become so compacted that its fossil nature cannot be detected by the naked eye. Microscopic examination of ground and polished sections usually reveals the cellular structure of plants. It was a time of great swamp lands with forests of fast-growing, soft-tissued, fernlike trees and dense undergrowth of smaller fernlike plants. The trees were very different from those existing today. Tall graceful **tree ferns** with high leaves rose to a height of 50 feet. The **scale-trees** were the largest plants of these ancient forests. They grew to a height of 100 feet and a diameter of 6 feet. Their name is due to the large and conspicuous scars which their leaf bases left upon the trunk. The forerunners of the modern conifers were slightly taller but more slender trees. Their leaves had the shape of blades and not needles like the pine trees of today. No fossil angiosperms have been found in the Paleozoic.

A conspicuous feature of the land plants of the Late Paleozoic is the occurrence of the same species in widely different parts of the world now separated by oceans. This is explained as due to their migration from one continent to another over land connections now submerged. The luxuriant, humid forests of the Late Paleozoic provided habitats for many new types of land and fresh-water animals. The great migration from the sea to the land had started in earnest. Land snails, spiders, and insects appear for the first time in the fossil record. Most remarkable were the **insects** (Fig. 40:6). Some four hundred or more different species are known, but they were strange primitive forms usually quite unlike any of those living today. The cockroaches were an exception for they seem to have been even more abundant then than today, and some species reached a length of 3 to 4 inches! What were probably the largest insects of all time — great dragonflies with a wing spread of over 2 feet — flew over the swamps of the coal forests.

It is, however, the amphibian fossils which characterize the Late Paleozoic and cause it to be called the **Age of Amphibians.** Eighty-eight different species are known from North America alone. They were nearly all small sprawling creatures, many only a few inches long. The largest was not greater than 10 feet over all. Like their forerunners of the Middle Paleozoic, they were stegocephalians and had heads encased in bony plates of armor.

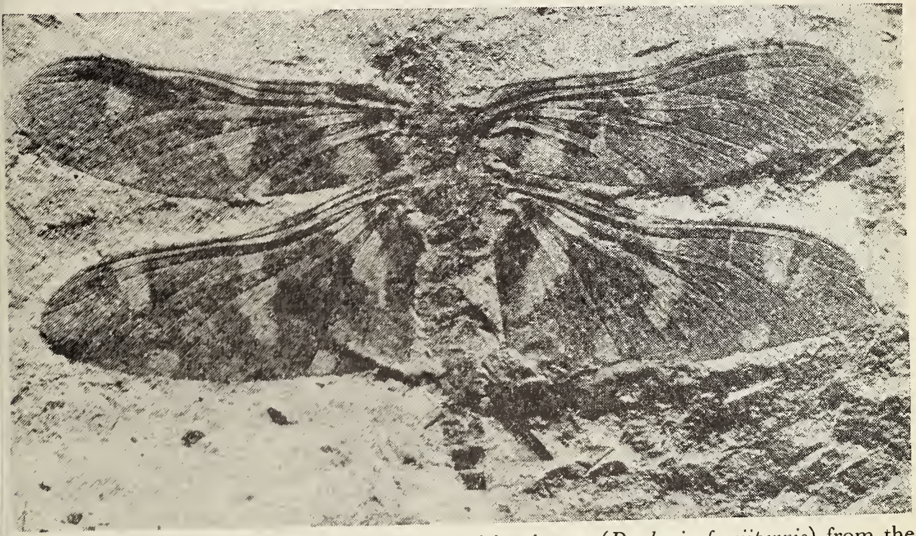

Fig. 40:6 Photograph of a fossil of a primitive insect (*Dunbaria fasciipennis*) from the Early Permian period (Late Paleozoic era). Reproduced by permission of the Peabody Museum of Yale University.

In the Late Paleozoic reptiles for the first time appear upon the scene. Most of the fossils represent long-bodied, long-tailed, and short-legged creatures. Of great interest are the **theriodonts,** short, thick-bodied reptiles which may have been closely related to the ancestors of the mammals. They carried their bodies clear of the ground. The bones of their skulls show a relationship to mammals.

An abundant and varied marine invertebrate fauna existed during the Late Paleozoic but some of the older forms like the trilobites which had been dominant in the early part of the era became extinct.

C. THE MESOZOIC ERA

The Mesozoic era is divided into the Early Mesozoic which includes the Triassic and Jurassic periods and the Late Mesozoic which consists of the Cretaceous period. The close of the Paleozoic era, it will be remembered, was marked by a complete retreat of the oceans from the land surface of the continent. It must have been a long time before the sea again encroached upon the land and left marine deposits, since the deposits of the Mesozoic reveal an entirely new fauna. The submergence of the land continued during the Early Mesozoic and even into the Late Mesozoic until fully half of the continent was covered by vast shallow arms of the sea. This was followed in the latter part of the Late Mesozoic by an emergence which carried the coast line to approximately its present position.

(1) THE EARLY MESOZOIC

The fossil plants of the Early Mesozoic like those of the end of the Paleozoic were pteridophytes and gymnosperms, but they had a somewhat more modern aspect, and we begin to recognize a resemblance to existing groups. Because the most characteristic plants of this time were the cycads this has been called the **Age of Cycads.** They were large palmlike plants with huge divided leaves. A few of them have lived on into modern times. They are, however, related, not to the modern palms, but to the conifers. Like them they bore staminate and carpellate cones and formed naked seeds.

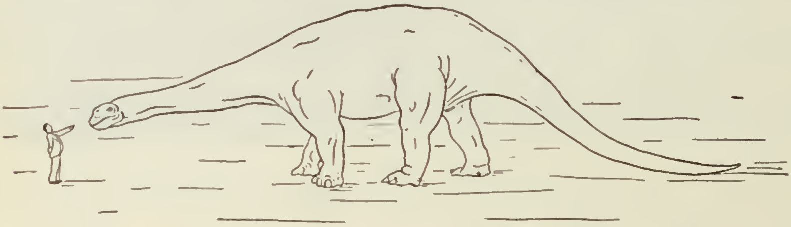

Fig. 40:7 *Brontosaurus*, a sauropod from the Upper Jurassic (Early Mesozoic) with a man drawn to the same scale, from a reconstruction in the American Museum of Natural History.

A thousand or more species of **insects** are known from the Early Mesozoic and most of the modern orders are represented — termites (Order Isoptera), grasshoppers and cockroaches (Orthoptera), cicadas (Hemiptera), caddis flies (Neuroptera), flies (Diptera), beetles (Coleoptera), bees, wasps, and ants (Hymenoptera). It is doubtful whether any of the fossils represent moths or butterflies, insects which in general depend for their livelihood upon flowering plants of which also we have no fossil record. The marine invertebrates resembled modern forms. The corals belonged to modern families. There were abundant gastropods and pelecypods (bivalves) resembling those of the present day, and numerous lobsters and shrimps. The cephalopods, curious shelled forms (ammonites and belemnites), would, however, look very strange in a modern aquarium.

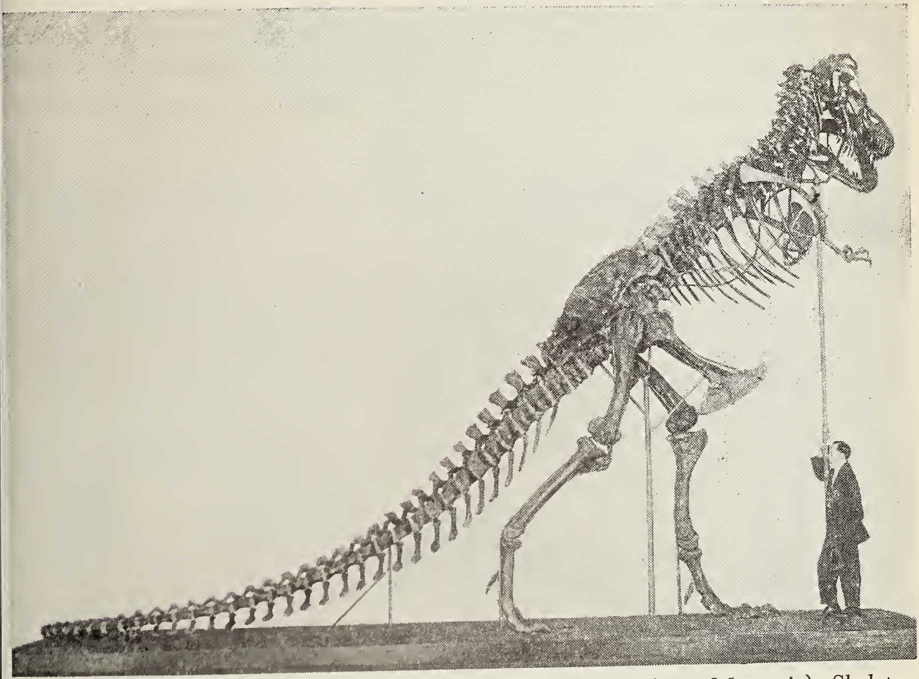

Fig. 40:8 *Tyranosaurus rex*, a theropod from the Cretaceous (Late Mesozoic). Skeleton in the American Museum of Natural History. Reproduced by permission.

Fossils of bony fishes (Teleostei) appear for the first time in the Early Mesozoic but they are rare compared with those of sharks and the ancient relatives of the sturgeon (Holostei). Lungfishes became rare. Amphibians were fairly numerous at the beginning of the Early Mesozoic and reached a large size, one form having a length of 15 to 20 feet and a skull 4 feet long. After this they gradually declined, becoming rare at the end of the Jurassic period and never again becoming prominent.

The Mesozoic is above all the **Age of Reptiles.** Already in the Early Mesozoic dinosaurs, pterosaurs, and ichthyosaurs ruled the land, the air, and the sea. The picture which the laborious excavation and restoration of the fossils of these bizarre and often gigantic creatures has given to the world is perhaps the most romantic that science has to offer.

Suddenly, as it seems in terms of geological time, they overwhelmed the earth and dramatized an era. From rather small beginnings in the Late Paleozoic they rose into prominence and reached their culmination in the middle of the Mesozoic.

The reptiles of the Mesozoic well illustrate a principle already discussed, namely, **adaptive radiation.** The reptiles of the Mesozoic radiated adaptively in three directions, the **dinosaurs** or "terrible-lizards" went out over the land, the **pterosaurs** or "winged-lizards" went into the air, and the **enaliosaurs** returned to the home of their ancestors, the sea.

The **dinosaurs** were terrestrial reptiles which walked with their bodies clear of the ground. Some species walked on all fours, other species adopted a bipedal gait with the body supported on the two hind legs and balanced by a long tail. They ranged in size from small forms 2½ feet in length up to the largest land animals of all time. From the many different types of dinosaurs a few are selected for description. The **sauropods** were large plant-eating dinosaurs with grinding teeth. Well-preserved skeletons have been found measuring 100 feet in length (Fig. 40:7). The **stegosaurs** were large dragonlike creatures with a

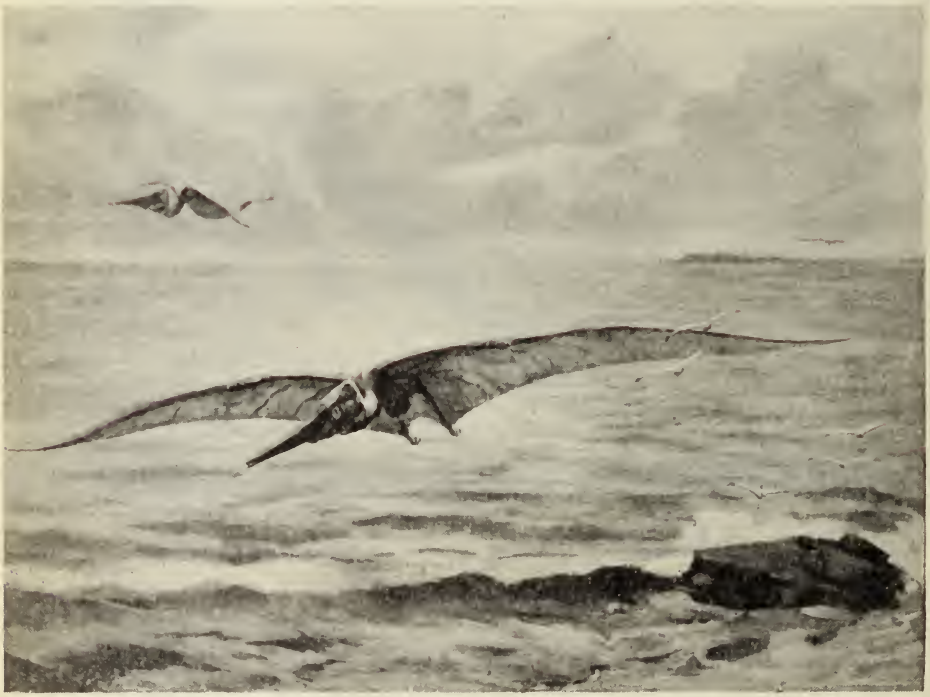

Fig. 40:9 *Pteranodon*, an enormous pterosaur which lived in the cretaceous period (Late Mesozoic era). From a photograph of a reconstruction made under the direction of Professor S. P. Langley in the United States National Museum. Reproduced by permission.

double row of bony plates extending along the back. The **theropods** were carnivorous dinosaurs with large heads and sharp teeth. They walked on their massive hind legs, using their smaller forefeet for grasping their prey (Fig. 40:8).

The **pterosaurs** were perhaps the most marvelous and strange of all the Mesozoic reptiles. The "little" fingers (fifth digits of the hands) formed long, jointed supports for membranous folds of skin which extended from them to the sides of the body and the hind legs and in the case of tailed forms to the tail, forming wings. One of these, Pteranodon (Fig. 40:9), had a wing spread of over 20 feet, about twice that of the largest known bird, but its body was scarcely larger than that of a turkey.

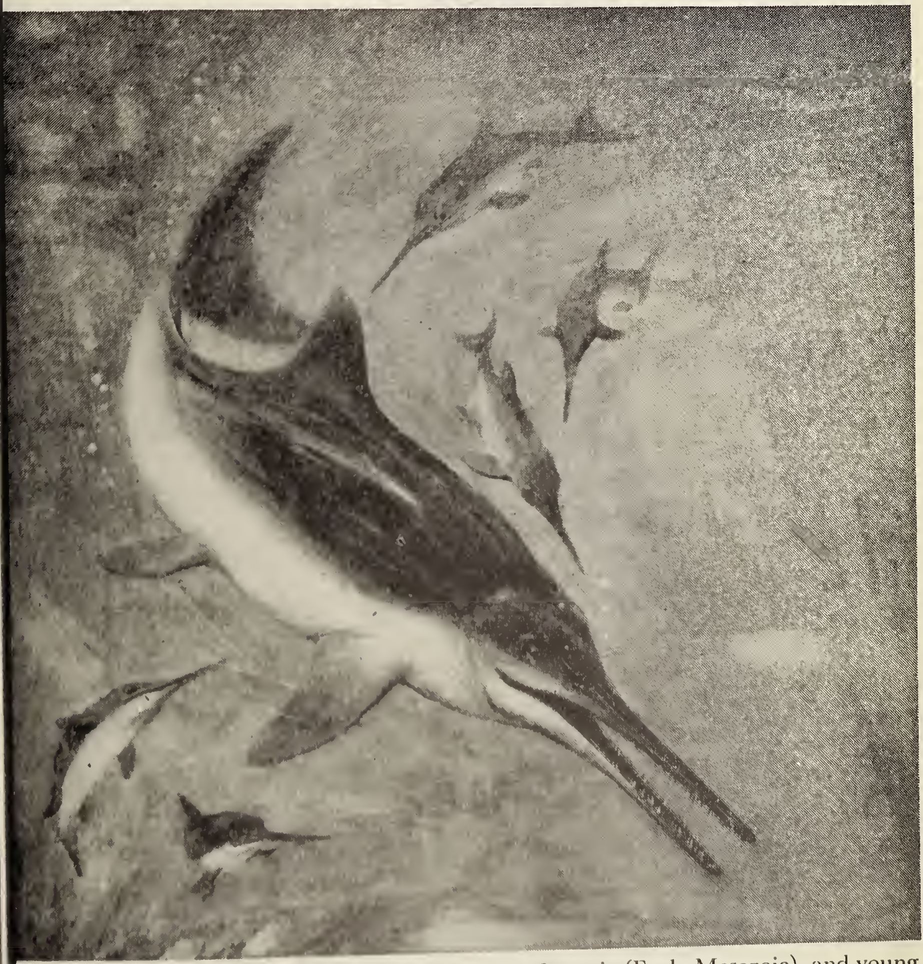

Fig. 40:10 *Ichthyosaurus*, an ichthyosaur from the Jurassic (Early Mesozoic), and young. Painted by Charles R. Knight under the direction of Henry Fairfield Osborn. Reproduced by permission of the American Museum of Natural History.

The **enaliosaurs** included the ichthyosaurs or fish-lizards and the plesiosaurs. The **plesiosaurs** were aquatic animals with heavy bodies, long slender necks, small heads, short tails, and powerful, paddlelike limbs. They lived on fish. The **ichthyosaurs** were more perfectly adapted to life in the sea and corresponded to the modern dolphins (which, however, are mammals). In appearance they were like large fish with long jaws and sharp teeth, and a tail and fins externally like those of a fish (Fig. 40:10). Most reptiles lay eggs and when they are aquatic return to land for breeding. The ichthyosaurs are known from the skeletons of

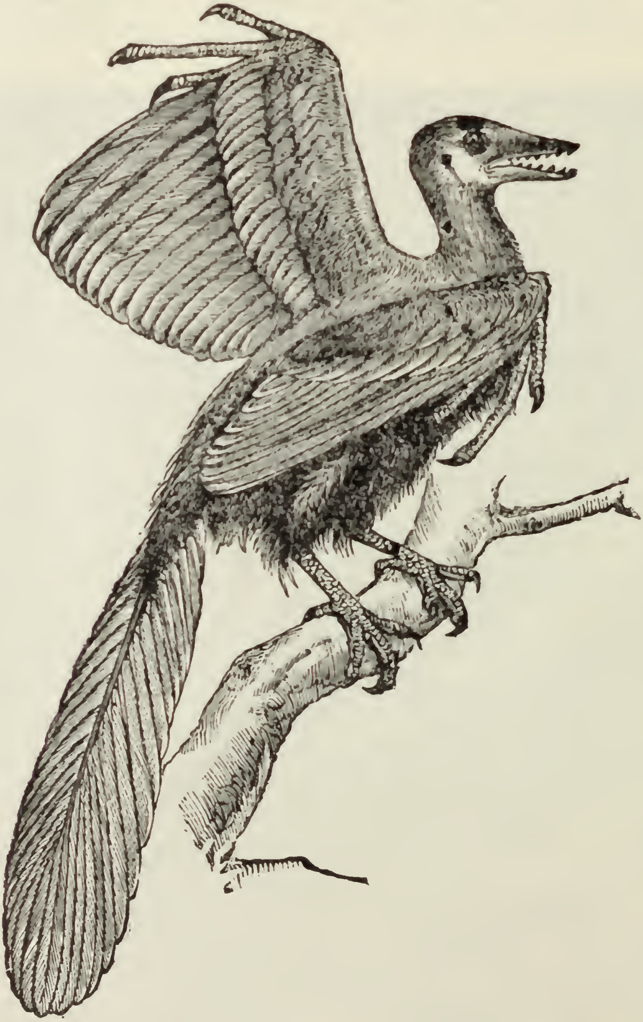

Fig. 40:11 A restoration of *Archaeopteryx*, a primitive bird from the Jurassic (Early Mesozoic). After Romanes, *Darwin and after Darwin;* from Haupt, *Fundamentals of Biology*, by permission of the Open Court Publishing Company and McGraw-Hill Book Company, Inc.

unborn young found within the ribs of the mother to have been viviparous.

Although reptiles dominated the scene in the Mesozoic, **birds** and **mammals** had already made a beginning in the early half of the era. The earliest known bird, Archaeopteryx, was about the size of a crow but in some respects was more reptilelike than birdlike. The beautifully preserved fossils of this animal show that it was covered with feathers and, therefore, was a bird, but it had claws on its wings and teeth in its jaws (Fig. 40:11). The earliest mammals, which are represented by fossils in rocks of the Early Mesozoic (Triassic), were small animals no bigger than a mouse or rat and were primitive forms resembling the Prototheria.

(2) THE LATE MESOZOIC

The Late Mesozoic is synonymous with the Cretaceous period. In this period fossil **angiosperms** appear in the rocks for the first time. They seem to have become abundant rather suddenly since by the end of the period they were the dominant group of plants. The species were different from those existing today but in some cases the genera were the same and we find the fossils of such plants as oaks, elms, maples, figs, palms, and grasses.

The various phyla of invertebrates which were established in the Paleozoic continued through the Mesozoic with certain changes in the types and their abundance.

Among the fishes, sharks became so abundant as to have left large numbers of fossil teeth. For the first time the bony fishes (Teleostei) became abundant and such genera as salmon, herring, bass, and cod appeared.

The rocks of the period contain relatively few fossils of amphibians and the group was probably not a conspicuous one during the latter part of the era.

Most of the reptiles of the Early Mesozoic continued into the Late Mesozoic. Some forms such as the snakes appear first as fossils in the rocks of the Late Mesozoic.

Some thirty or more species of toothed birds are known by their fossils from the Late Mesozoic. One of these was a small shore bird with powerful wings. The others were large diving birds, like the modern penguins and probably like them incapable of flight.

The mammalian fossils found in the rocks of the Late Mesozoic indicate that as in the early part of the era these animals were small, primitive, and rare.

The close of the Mesozoic era has been called **The Time of the Great Dying,** for many groups of animals which flourished during most or a part of the era are either not represented among the fossils of the next era or, if so, only rarely. Not one of the many different types of dinosaurs is known to have lived into the next era. The pterosaurs attained their wonderful and highly specialized adaptation to flight only, as it appears, to soon disappear from the record. The marine reptiles such as the ichthyosaurs and plesiosaurs also became extinct at the end of the era. Of all the vast reptilian horde which roamed and dominated the surface of the earth for a hundred million years or more there survived into the Cenozoic but a few lizards, snakes, crocodiles, and turtles, fewer probably than we have with us today. Death and extinction was not, however, confined to reptiles; among invertebrates certain groups of mollusks also disappeared from the record. Precisely what was the cause of the decline and extinction of these dominant and diverse groups, whether it was the change to a cooler and more rigorous climate, the advent of a new type of vegetation, the vanishing of the swampy lowlands, or some peculiarity in their organization, or all of these and more combined is largely a matter of speculation.

D. THE CENOZOIC ERA

The Cenozoic is the era in which we live. During the time which it includes the surface of the land acquired most of its present features and the continents their present contour. The Cenozoic is divided into two periods, the earlier of which is called the **Tertiary,** the later, the **Quaternary.** These are old terms which have come down from the early days of the science of geology when the rocks were divided into Primary (which included those of the Archeozoic, Proterozoic, and Paleozoic eras), Secondary (which included those of the Mesozoic), Tertiary, and Quaternary. The last two divisions have been retained but they are recognized as periods and grouped together in the Cenozoic. In the Tertiary, mammals succeeded reptiles as the dominant animals and for this reason the period has been called the Age of Mammals. For a similar reason the Quaternary has been called the Age of Man.

(1) THE TERTIARY PERIOD

As we approach the present in our study of the history of life on the earth, the fossil record becomes more extensive and detailed and it is convenient to divide the periods into shorter intervals of time which are called **epochs.** The Tertiary period is divided into four epochs which are named, beginning at the most ancient, the **Eocene, Oligocene, Miocene,** and **Pliocene.**

We have already seen that the angiosperms attained a dominant position among plants toward the end of the Mesozoic. This position they have maintained with certain changes to the present time. During the Tertiary forests of such trees as the maple, fig, and cypress occurred as far north as Greenland and Spitzbergen, indicating that the climate of North America and Europe was in general milder than it is today. Although grasses are very seldom found fossil there is, in the grinding teeth of many of the mammals of the time, good evidence of vast, grass-covered prairies as early as the middle of the Tertiary. The deciduous trees, herbs, and grasses provided a new environment for all kinds of land life.

Fossil insects have been found in much greater adundance in the rocks of the Tertiary than at any previous time. In a single stratum of Miocene rocks near a small town in Switzerland over nine hundred different species have been found. Some two thousand different species of insects have been found beautifully preserved in amber in rocks of Oligocene time on the shore of the Baltic.

The modern bony fishes predominated during the Tertiary but sharks of great size, up to 60 or 80 feet in length were abundant as shown by their fossil teeth in rocks of the period on the east coast of the United States.

Many of the modern types of birds appear as fossils of this period, but a curious feature is the wide occurrence of gigantic flightless forms resembling the existing ostriches.

Interest centers in the remarkable **adaptive radiation of mammals** which has given to the period the designation **Age of Mammals.** As previously noted the earliest fossil mammals occur in rocks of the Early Mesozoic (Triassic) and represent small and unspecialized forms. While the dinosaurs were dominant the mammals seem to have made little progress, for the fossils of the end of the Mesozoic represent mammals of the same primitive type as those of the early part of the era.

The beginning of the Cenozoic (Eocene) saw the rise of the **archaic mammals,** and the **first mammalian adaptive radiation.** These animals came to occupy the various habitats and modes of getting a living left vacant by the extinction of the dinosaurs. Some of the archaic mammals reached a large size and attained a considerable degree of specialization, yet the group as a whole retained three important primitive characters: Their teeth were simple and relatively undifferentiated, and there was usually the primitive number of forty-four, eleven on each side of each jaw, indicating that they had not become adapted to a particular diet; they walked on the soles of their fore and hind feet, both of which had five digits, the primitive number, indicating that they had not become adapted to a particular habitat; their skulls contain a relatively small cranial cavity, with an especially small portion for the cerebral hemispheres, indicating that the brain was small and the "intelligence" of a low order. Nevertheless, these archaic forms must be regarded as the first great attempt of mammals to dominate the world. Although several orders of archaic mammals are distinguished with forms imitating existing bears, cats, and rodents, none of the orders with the possible exception of the insectivores seems to have persisted to the present day. One order (Creodonta) is believed to have given rise to the modern carnivores.

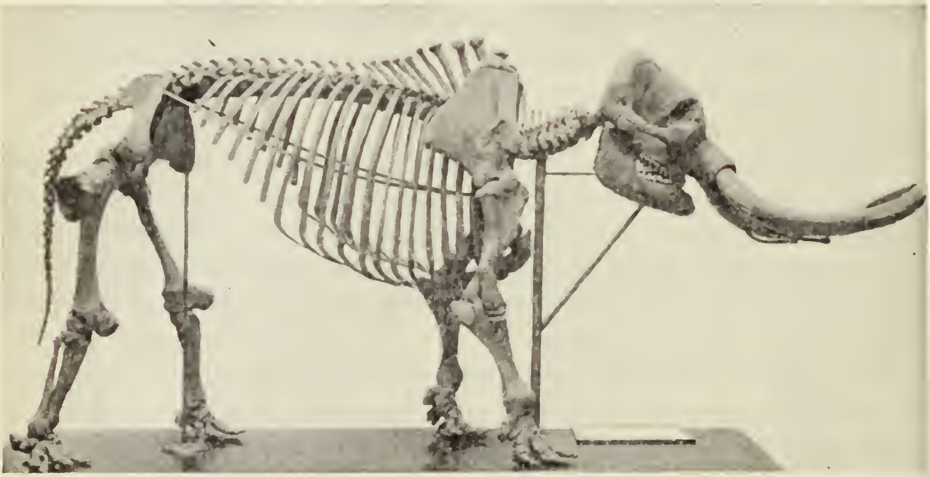

Fig. 40:12 The skeleton of a mastodon, a proboscidian from the Pleistocene (Quaternary period), found at Cohoes, N. Y. Photograph of the specimen in the New York State Museum at Albany.

At this period we find existing side by side with the archaic mammals, which still held the center of the stage, a number of primitive forms which are recognized as ancestral to the modern orders. These were all small animals, none of which would have reached to a man's waist. They include little four- and three-toed horses, tiny camel-like animals, squirrel-like rodents, and small monkeys.

By the **Oligocene** many of the modern orders of mammals had become established and most of the archaic forms had become extinct.

In the **Miocene,** mammals reached the height of their development. Horses, camels, rhinoceroses, and giant pigs were abundant, various kinds of rodents and carnivores were present. An ape allied to the gorilla occurred in Europe and Asia.

During the **Pliocene,** mastodons, great elephant-like creatures, migrated from Europe to North America across a land bridge which then connected Alaska and northern Asia (Fig. 40:12). Rhinoceroses were particularly abundant in Nebraska.

(2) THE QUATERNARY PERIOD

The Quaternary is known as the **Age of Man** for in this period man appears upon the scene and becomes the dominant form of life.

The **Pleistocene** epoch includes the greater part of the Quaternary period. During this epoch the Northern Hemisphere underwent a series of glacial stages or ice ages separated by warmer interglacial stages. Four of these glacial stages separated by three interglacial stages are recognized. The epoch in which we now live, called the **Recent Epoch,** follows the last of four glacial stages and, for all we know, may be merely a fourth interglacial stage. By some authorities this short interval of time, which can scarcely be more than twenty-five thousand years, is elevated into a geological era, the Psychozoic era, presumably because of the vast changes which the dominance of man has brought about on the surface of the earth; changes, however, which a fifth glacial stage would do much to obliterate.

At the time of its greatest extent the great ice cap which covered North America extended over all of Canada, the Great Lakes, New England, New York State, and through Ohio, Michigan, Indiana, Illinois, Wisconsin, and Minnesota to the banks of the Ohio and Missouri rivers. This great sheet of ice was, in all probability, similar to that which covers Greenland today. The interglacial stages occurred when the ice cap retreated toward the north and left a fertile land with a climate at times milder than that of the present.

During the Pleistocene the mammalian fauna of North America was as varied in size and type as that of Africa now is. Great herds of woolly mammoths ranged over the ice, crossing back and forth from Alaska to Siberia. Some, as already stated, became frozen into the great ice sheet to be thawed out some twenty-five thousand years later. These animals were so numerous that their tusks, still found imbedded in the frozen soil, provide half the world's ivory. Further south a number of different species of buffaloes roamed the plains and at least ten species of horses grazed upon the grasslands. On these herbivores, a multitude of carnivores preyed, wolves, foxes, bears, the giant saber-toothed tiger, with a tusk 6 or 8 inches in length, and many other types. From South America came the giant armadillos and ground sloths, curious backward forms which developed in that continent when it was isolated by the submergence of the Isthmus of Panama. During the glacial epochs the mammals of North America moved southward as the climate grew colder. Thus the walrus, which we regard as an arctic form, migrated in the Pleistocene as far south as the coast of Georgia. During the interglacial periods, tropical animals migrated northward. The manatee, for example, which now occurs on the Florida coast, migrated during the Pleistocene as far north as the coast of New Jersey.

There are no certain records of the presence of man or any other primates in North or South America during the Pleistocene. For the earliest traces of man, as for so much of his subsequent history, we must turn to the Old World. A later chapter (Chapter 44) is devoted to the fossil record of man and the primates.

5. SUMMARY OF THE CHIEF BIOLOGICAL FEATURES OF THE GEOLOGICAL RECORD

Life has existed on the earth for an incredibly long time, probably at least 1,500,000,000 years. It is possible to divide this time into five eras. During the first two eras, the Archeozoic and the Proterozoic, which represent two-thirds of the total time, the record shows the existence of only such primitive forms as the Protozoa (Radiolaria) and the Porifera (sponges). In the Early Paleozoic there burst upon the scene (the bursting took a hundred million years or so) the great adaptive radiation of the trilobites. In the Middle Paleozoic appear the first land plants and the first true fishes, the latter showing in the Devonian a great adaptive radiation of Elasmobranchii and Dipnoi. In the Late Paleozoic amphibians became abundant and the first reptiles appeared. In the Mesozoic occurred the great adaptive radiation of reptiles when dinosaurs, pterosaurs, and enaliosaurs were abundant. In this era the first birds and the first mammals appeared and insects became common. The Cenozoic saw the first adaptive radiation of the primitive mammals and later the adaptive radiation of modern mammals. Toward the end of this era man appeared.

From the point of view of evolution this record shows certain very interesting features. Of great significance is the **order in which the different groups are found in the geological record.** First appear the Protozoa and Porifera, next the other groups of invertebrates, then, and only then, the vertebrates. The order in which the vertebrates appear is especially significant since the record is so complete — fishes, amphibians, reptiles and, almost simultaneously, birds and mammals.

Of almost equal interest is **adaptive radiation.** The fossil history of most groups of animals and plants begins with a few, often small, primitive forms, then adaptive radiation occurs, they begin to invade new areas, and to become differentiated into new species and genera adapted and specialized to meet the new conditions. Eventually the earth becomes overrun with a multitude of new forms, all conforming more or less to the main structural plan of the original primitive type. Striking examples of adaptive radiation are to be found in the case of the trilobites, Devonian fishes, Mesozoic reptiles, and archaic and modern mammals, but the story is the same wherever there is an extensive record of the group. It may be added in passing that there is usually only one adaptive radiation of any group and that after this has reached its climax the group tends to decline in numbers of species. It would be interesting to know what the next great adaptive radiation is going to be.

These two features, adaptive radiation and the order in which the groups appear, are satisfactorily explained by the theory of organic evolution, the more specialized and structurally complex forms being descended from simpler, less complex forms.

The progress of life upon the earth — the march of evolution — has not been steady and even, no more than have the geological changes with which it has been associated progressed always at the same rate. During certain periods, particularly those in which great adaptive radiations occurred, the progress of evolution has been fast and the realm of life has rapidly expanded. During other periods when conditions seem to have been less favorable to living things progress was slow. The alternation of periods of more rapid with periods of less rapid evolution of life upon the earth has been called the **pulse of life.**

Topical Outline of Chapter 40

1. How the record was made 809
    A. How fossils are formed 809
        (1) Preservation of the actual organism 809
        (2) Petrifaction (preservation by chemical change) 809
        (3) Molds and casts 810
        (4) Footprints and trails 811
    B. Conditions favoring fossilization 811
    C. The chance of a fossil occurring 811

  - D. The formation of sedimentary rocks 812
- 2. Piecing the record together 813
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Questions

1. What is a fossil?
2. Classify fossils according to their method of preservation.
3. What conditions favor the formation of a fossil? What conditions tend to preclude its formation?
4. How are sedimentary rocks formed? What is an unconformity? How may this condition arise?
5. State the law of superposition.
6. Explain why fossils may be used to identify strata.
7. Construct a geological timetable.
8. Explain the uranium-lead ratio method of determining the age of a rock.
9. What fossils, if any, have been discovered in the Archeozoic and Proterozoic eras?
10. What two groups of animals were most abundant in the Early Paleozoic?
11. What evidence is there of migration to the land in the Middle Paleozoic?
12. Give an account of the land plants of the Late Paleozoic.
13. What insects occurred in the Paleozoic and in which part of the era? Where do reptiles first appear in the record?
14. Give a short account of the plants of the Mesozoic.
15. Discuss adaptive radiation as applied to Mesozoic reptiles.
16. When do spermatophytes first appear? When do angiosperms first appear?
17. When was the "Great Dying"?
18. Name in order the epochs of the Tertiary.
19. When did the first mammalian adaptive radiation occur? What were some of the forms which occurred in this radiation?

20. When did mammals reach the height of their development?
21. Give a short account of the Pleistocene fauna of North America.

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CHAPTER 41

The History of the Theory of Evolution

1. THE MEANING OF THE TERM "EVOLUTION"

"Evolution" is a much-abused word — abused by many popular misconceptions and popular prejudices. It is therefore important to understand the scientific meaning of the term. Etymologically the word means an "unrolling" or "unfolding." This original meaning has been extended and generalized. In its most general connotation the word "evolution" is applied to the whole universe and when so used implies that gradual and orderly change from the simple to the complex is the law of nature, that this principle has governed the form and movements of the stars, the changing surface of the earth, and the long pageant of living creatures that have lived and died on it. According to this conception there has been an evolution of the inorganic world — an evolution of the stars and other heavenly bodies, of the surface of the earth, including the oceans and the atmosphere. There may even have been an evolution of the chemical elements from electrons, protons, and neutrons. This aspect of the evolutionary principle may be called **inorganic evolution.** The same idea is carried into the realm of living things, i.e., the great complexity and variety of the organic world is explained as due to the gradual modification of simpler organisms into more complex and highly differentiated forms. This is the principle of **organic evolution.**

It is concerning the principle of organic evolution that there has been most controversy and it is the application of the principle of evolution to plants and animals including man which has had most effect upon modern thought. The principle of organic evolution is concerned with the problem of how the great multitude of different kinds of living organisms came into being, i.e., with the origin of species.

Two main types of theories have been advanced to account for the origin of species; either each species was created individually by some unseen and presumably supernatural power (special creation) or, life once having appeared upon the earth, the various species have risen one from another by a gradual process of modification extending through untold generations (organic evolution). Whether or not one is prepared to admit only these two alternatives, and whether or not he believes them to be mutually exclusive, the statement of the problem in this form helps to clarify much of the argument in the case.

2. GREEK AND ROMAN THEORIES OF EVOLUTION

It is a popular misconception that the idea of organic evolution is a recent and radical theory which seeks to supplant a traditional belief. In reality the idea of evolution in various crude and indefinite forms is as old as that of special creation. The early history of the idea of evolution is well told in *From the Greeks to Darwin* by H. F. Osborn. The philosopher, Thales (640–546 B.C.), "declared water to be the matter from which all things arose, and out of which they exist. This idea of the aquatic or marine origin of life, which is now a very widely accepted theory, is therefore an extremely ancient one." Anaximenes (588–524 B.C.) "introduced the idea of primordial terrestrial slime, a mixture of earth and water, from which, under the influence of the sun's heat, plants and animals and human beings were directly produced." Aristotle was not only one of the great philosophers but he was also one of the founders of the biological sciences. "Aristotle's theories as to the origin and succession of life" carried him far beyond the facts, into discussions of a purely metaphysical nature. Nevertheless he emphasized the idea of a gradual change from the simple and, as he expressed it, "imperfect," to the more complex and "perfect," and he is to be regarded as one of the founders of the principle of evolution. Epicurus (341–270 B.C.) contributed to the idea of evolution by his insistence on natural, as opposed to supernatural, causes. The Latin poet Lucretius (99–55 B.C.) in his great evolutionary poem *De Rerum Natura* draws a picture of how he imagined plants and animals to have arisen from Mother Earth.

> And first the race she reared of verdant herbs,
> Glistening o'er every hill; . . .
> . . . and the trees
> Felt the deep impulse, and with outstretched arm
> Broke from their bonds rejoicing; . . .
> . . . Then, in order next
> Raised she the sentient tribes, in various modes,
> By various powers distinguished; for nor heaven

> Down dropped them, nor from the ocean's briny waves
> Sprang they, terrestrial sole.[1]

Lucretius advanced the mechanistic as opposed to the vitalistic conception of nature.

During the centuries which followed the classical period, learning was largely in the hands of the church. The great Christian Father, Saint Augustine (A.D. 353–430) interpreted the first chapter of Genesis as stating that in the beginning matter was created with the properties and potentialities to evolve into the animate and inanimate worlds as we see them today. We would express it today by saying that the Creator acted as the first cause giving to matter the power to evolve. One authority has stated that "Augustine distinctly rejected Special Creation in favor of a doctrine which, without any violence to language, we may call a theory of Evolution." [2]

3. EVOLUTION IN THE SEVENTEENTH CENTURY

With the seventeenth century, the century of Francis Bacon, William Harvey, Marcello Malpighi, Jan Swammerdam, and Antony von Leeuwenhoek, began a new epoch in the history of biology and a new era in the development of evolutionary theory. Francis Bacon (1561–1626) in the *Novum Organum*, a treatise on scientific procedure, outlined the possibilities of the inductive method. William Harvey demonstrated the power of the experimental method to solve physiological problems by applying it to the circulation of the blood. Malpighi, Swammerdam, and Leeuwenhoek showed what might be achieved by accurate observation and minute analysis in the discovery of the corpuscles of the kidney, blood capillaries, the spermatozoon, and bacteria.

4. EVOLUTION IN THE EIGHTEENTH CENTURY

These men were followed in the eighteenth century by the great naturalists Buffon and Linnaeus. George Louis Leclerc Buffon (1707–1788) was a prolific and suggestive writer on natural history whose books were widely read. He is to be regarded as an evolutionist for he believed in the mutability or changeableness of species, although he did not attempt to give any formal proof of the theory. Linnaeus has already been referred to as the founder of the binomial method of nomenclature. In contrast to Buffon, Linnaeus had a very exact and systematic mind. He believed in the fixity of species and in special creation.

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[1] Quoted from H. F. Osborn, *From the Greeks to Darwin*, The Macmillan Company, New York, 1913.

[2] Moore, Aubrey, *Science and Faith*, London, 1892.

5. EVOLUTION AT THE BEGINNING OF THE NINETEENTH CENTURY

Again at the end of the eighteenth and the beginning of the nineteenth century two contrasting personalities with widely different points of view stand out, Lamarck and Cuvier. Jeanne Baptiste Pierre Antoine de Monet, better known as the Chevalier de Lamarck (1744–1829), was a gifted zoologist and facile writer who devoted most of his life to the study of invertebrates. It is, however, for his contribution to the theory of evolution that he is best known. H. F. Osborn considers that Lamarck, as the founder of a complete modern theory of descent, is the most prominent figure between Aristotle and Darwin. As Lamarck's contribution to the theory of evolution concerns particularly the mechanism of evolution, his work will be discussed in a subsequent chapter. Cuvier was a great zoologist and one of the founders of morphology. He was an opponent of Lamarck and of the evolution theory, believing in the fixity of species.

In the early part of the nineteenth century the idea and the implications of the evolution theory seem to have taken more definite form. Two questions were prominent in the discussions of the time: **catastrophism** versus **uniformitarianism**, and fixity versus mutability of species, and it became apparent that on the answers to these two questions rested the truth or falsehood of the evolution theory. According to the "catastrophists" there occurred during the history of the earth a number of cataclysms or violent catastrophes during which all living things were destroyed. In the intervals between the cataclysms the earth was restocked by special creation with new forms of life which were in turn destroyed and buried at the next cataclysm. Uniformitarianism at first seems to have implied that the earth, and the life upon it, had no beginning and would have no end, but latterly it came to be practically equivalent to evolution as applied to geology. There is no doubt that in the early part of the nineteenth century the catastrophists had it all their own way.

6. LYELL, DARWIN, AND WALLACE

The man who more than any other was responsible for the overthrow of catastrophism was Charles Lyell (1797–1875). In *Principles of Geology*

(1830–1832), one of the great classics of science, he laid the foundation for the modern science of earth structure. Lyell overcame opposition by the clarity of his reasoning and the charm of his literary style. Through the influence which his work and his personality had on Charles Darwin, Lyell must be regarded as an important contributor to the theory of organic evolution.

The name of Charles Darwin (1809–1882) so much overshadows those of all the other contributors to evolutionary thought that even to the present day evolution is often referred to as the Darwinian theory. Darwin was born at Shrewsbury in England and at an early age showed an interest in observing and collecting natural objects. He was sent, at the age of sixteen, to Edinburgh University to study medicine. After two years there, in which he showed more interest in biology and natural history than in the healing art, he went to Cambridge University with the object of becoming a minister of the gospel. Here again his chief interest was in geology, botany, and zoology. Darwin's real scientific education began when, in 1831, soon after his graduation from Cambridge, he went on an exploring trip round the world on "His Majesty's ship Beagle," a "ten-gun brig." The voyage on the little sailing ship lasted five years and Darwin worked incessantly, reading when at sea and when on land making excursions into the interior to collect and make notes, both geological and biological.

When Darwin returned to England he made the acquaintance of Lyell and the next ten years were devoted to working up the notes and collections made on the voyage. During his explorations on the voyage around the world Darwin thought much on the origin of species and continued to do so after his return as he reread his notes with his collections before him. As he expressed it, "I then saw how many facts indicated the common descent of species," and again, "It occurred to me in 1837, that something might perhaps be made out on this question by patiently accumulating and reflecting on all sorts of facts which could possibly have any bearing on it." In July of the same year "he opened his first notebook on the subject." Some months after this Darwin read the *Essay on the Principle of Population*, by Thomas Malthus, a work which aimed to show that the population of any area is limited by the supply of food and other necessities of existence. The idea of a struggle for existence developed in his mind and he continued methodically and patiently to collect facts. Twenty-two years later, in 1859, *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life* appeared. The main thesis of this work can scarcely be better expressed than in the words of Thomas Henry Huxley, its greatest exponent.

"All species have been produced by the development of varieties from common stocks: by the conversion of these, first into permanent races and then into new species, by the process of natural selection, which process is essentially identical with that artificial selection by which man has originated the races of domestic animals — the struggle for existence taking the place of man, and exerting, in the case of natural selection, that selective action which he performs in artificial selection."

The idea of natural selection developed by Darwin in his theory of the origin of species was not entirely new. It is to be found in the works of Lyell and certain other of Darwin's predecessors. While Darwin was patiently collecting his facts another man, Alfred Russel Wallace, also imbued with Lyell's *Principles of Geology*, was meditating on the problem of the origin of species, while collecting in the East Indies. Darwin's title to fame rests on the tremendous accumulation of facts which he brought to bear on the problem and the judgment and clarity with which he presented the argument.

Darwin was not connected with any university, research, or other institution. He lived most of his life and did most of his work on a country estate called Down, near the village of Bromley in the South of England. As the fortunate possessor of a moderate income he was able to devote his entire time and effort to his researches. Although handicapped throughout the greater part of his life by ill-health, Darwin lived to have "the satisfaction of knowing that the doctrine of evolution had come to be — mainly through his own great efforts — the accepted creed of all naturalists and that even for the world at large it had lost its imaginary terrors."[1] As Thomas H. Huxley wrote, "None have fought better, and none have been more fortunate, than Charles Darwin. He found a great truth trodden underfoot, reviled by bigots, and ridiculed by all the world; he lived long enough to see it, chiefly by his own efforts, irreparably established in science, inseparably incorporated with the common thoughts of men, and only hated and feared by those who would revile, but dare not. What shall a man desire more than this?"

7. EVOLUTION ESTABLISHED AS A PRINCIPLE OF NATURE

After the heated, largely prejudiced, and often ill-informed criticism which greeted the publication of the work of Darwin and Wallace had subsided, and after the confusion of thought and the violent argumentation had given way to patient and careful investigation the "theory of evolution" began to emerge as a fundamental principle of biological science. As a great unifying idea it stimulated investigation in all those branches of science which could contribute to its confirmation and elaboration. Considering the difficulty of the problems which the study of evolution presents, and considering that the whole realm of organic nature is included, great progress has been made since Darwin's time and especially since the beginning of the present century.

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[1] Judd, John W., *The Coming of Evolution*, Cambridge University Press, London, 1912.

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1. The meaning of the term "evolution" 838
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5. Evolution at the beginning of the nineteenth century 841
6. Lyell, Darwin, and Wallace 841
7. Evolution established as a principle of nature 843

Questions

1. Explain the meaning of the term "evolution," giving as an example what you imagine has been the course of evolution of some higher animal.
2. Contrast the theory of evolution with the theory of special creation.
3. Discuss Greek and Roman theories of evolution.
4. What were the ideas of Buffon and Linnaeus, Lamarck and Cuvier, on evolution?
5. What were the relations of Lyell, Darwin, and Wallace to the development of the theory of natural selection?
6. Write a brief account of Darwin's life.

Suggestions for Further Reading

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CHAPTER 42

The Evidences for Organic Evolution

In considering organic evolution we must clearly distinguish between the evidences of its having occurred and its possible causes. The difference between evidences and causes may be illustrated by a familiar example. Evidences that A had been at a particular restaurant would be a statement by B that he had seen him in the restaurant, or the finding of his gloves there. Causes for his having been there might be that he was hungry, or that he wanted to entertain a friend. We will consider in this chapter evidences of evolution. In many cases the facts which provide these evidences have been already discussed and their value as evidence of evolution will have already occurred to the student. It will be valuable, however, to collect them together into a systematic argument.

1. CLASSIFICATION

The principles of classification have been discussed in Chap. 2 and the natural system of classification of plants and animals has been outlined in that chapter and in more detail in the appendix. We are concerned here with the evidence which these classifications provide for the theory of evolution. The argument has never been better presented than by Darwin in the *Origin of Species.*

> From the most remote period in the history of the world organic beings have been found to resemble each other in descending degrees, so that they can be classed in groups under groups. This classification is not arbitrary like the grouping of the stars in constellations.
>
> Naturalists, as we have seen, try to arrange the species, genera, and families in each class, on what is called the Natural System. But what is meant by this system? Some authors look at it merely as a scheme for arranging together those living objects which are most alike, and for separating those which are most unlike; or as an artificial method of enunciating, as briefly as possible, general

propositions — that is, by one sentence to give the characters common, for instance, to all mammals, by another those common to all carnivora, by another those common to the dog-genus, and then, by adding a single sentence, a full description is given of each kind of dog. The ingenuity and utility of this system are indisputable. But many naturalists think that something more is meant by the Natural System; they believe that it reveals the plan of the Creator; but unless it be specified whether order in time or space, or both, or what else is meant by the plan of the Creator, it seems to me that nothing is thus added to our knowledge. Expressions such as that famous one by Linnaeus, which we often meet with in a more or less concealed form, namely, that the characters do not make the genus, but that the genus gives the characters, seem to imply that some deeper bond is included in our classifications than mere resemblance. I believe that this is the case, and that community of descent — the one known cause of close similarity in organic beings — is the bond, which though observed by various degrees of modification, is partially revealed to us by our classifications.

This becomes clear when we consider the principles or rules adhered to in classification and what types of characters are considered to be of most importance. In distinguishing large groups the general plan of structure and life cycle of the whole organism is regarded of most importance; thus such characters as an endoskeleton, dorsal nervous system, and gill clefts in the embryo are chosen to distinguish the phylum Chordata from the other phyla of the animal kingdom, and in the plant kingdom the division Spermatophyta is distinguished from the other divisions by the occurrence of the seed in the life cycle and the structure of the sporophyte, vascular bundles, and floral structure. When we come to smaller groups and wish to describe genera and species the characters chosen are more superficial and show more variation with the mode of life of the organism. Thus in distinguishing the different species of warblers, the color and markings of the feathers, and to a less extent the size, are almost the only structural features used, and in distinguishing the different kinds of oaks the shapes of the leaves and acorns and the appearance of the bark are of importance. There are also characters which vary from individual to individual. This would be expected if all organisms have been descended from one or a few simple forms. Those most closely related would differ only by minor and superficial characters, while those more distantly related would show more fundamental differences.

The argument can be put in a simpler but cruder form. If the different species now existing on the earth were descended from a few simpler forms, then one would expect to be able to classify them into phyla, classes, orders, families, genera, and species just as is now done. On the other hand it is difficult to imagine how this would have been possible were the organisms not related by descent but each specially created according to individual plans.

Another kind of evidence arises from the attempt to define a species. Taxonomists are by no means agreed upon a definition of the term "species." To what extent must individuals differ to be placed in different species? What extent of resemblance justifies their being placed in the same species? The question is not simplified by the creation of subspecies and varieties within the species or subspecies. From a very extended study of the oaks of the world the French botanist, A. de Candolle, concluded, "They are mistaken, who repeat that the greater part of our species are clearly limited, and that the doubtful species are in a feeble minority. This seemed to be true, as long as a genus was imperfectly known, and its species were founded upon a few specimens, that is to say, were provisional. Just as we come to know them better, intermediate forms flow in, and doubts as to specific limits augment." He also adds that it is the best known species which present the greatest number of spontaneous varieties and subvarieties. Thus *Quercus robur* has twenty-eight varieties, all of which, excepting six, are clustered round three subspecies, namely *Q. pedunculata*, *sessiliflora*, and *pubescens*. The forms which connect these three subspecies are comparatively rare; and, as Asa Gray again remarks, "if these connecting forms which are now rare, were to become wholly extinct, the three subspecies would hold exactly the same relation to each other, as do the four or five provisionally admitted species which closely surround the typical *Quercus robur*."

Several studies of snails have been made in recent years with this problem in mind. In each case the presence of **intergrading species,** i.e., species with characters intermediate between those of two other species, have been found. These facts show that evolution is a continuous process and that whenever a careful study is made of a small group of plants or animals it can be seen in progress. Subspecies and varieties are new species in the process of formation.

2. HOMOLOGY

In the study of the frog and man, system after system was compared in detail and the close correspondence in general plan and often in details of structure was seen to be remarkable. The skeletons were not only similar in their minute structure, but in many instances there was a bone for bone correspondence. The digestive systems showed such differences as might be expected from the different modes of life of the two animals, but in general the resemblances were more conspicuous than the differences. And so one might go on through the series of systems.

This correspondence was expressed by the term **homology.** Organs or other bodily structures in individuals of two different species are said to be homologous when they show the same type of structure, the same relation to the other organs of the body, and a close similarity in their embryological origin and development (Fig. 42:1). Why are organs which serve such different functions as walking, running, swimming, flying, constructed on the same plan? Why did the wings of a pterosaur contain the same bones as the forefeet of a theropod? Why do the wings of a bat contain the same bones as the forefeet of a dog, or the hand of a man? And why does a whale breathe by means of lungs in the middle of the ocean? The natural explanation is descent from a common simpler type which gradually became modified while retaining fundamental features, these fundamental features being such as could not become greatly modified without interfering with the vital processes of the individual. Thus in the bat the framework for the wing arose as a result of a gradual elongation of the bones of the fingers rather than from the development of an entirely new bony structure adapted from the beginning to flight.

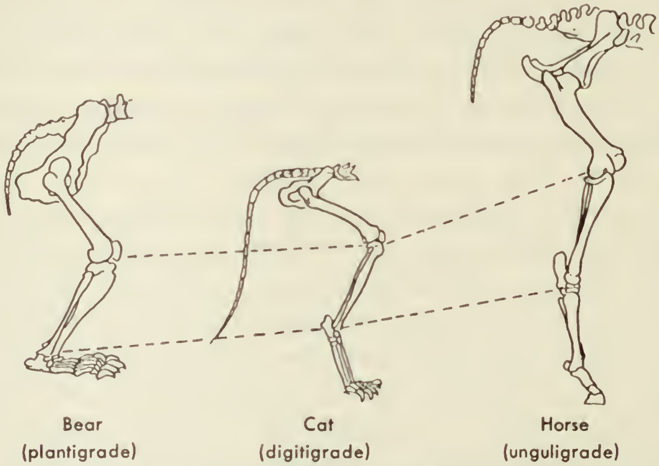

Fig. 42:1 The hind limbs of the bear, cat, and horse showing the homologies of the different parts and bones. The upper dotted line joins the knees, the lower the ankles.

Again when the wing of a bat is compared with that of a bird, why the marked difference? The bat was first a mammal and then a chiropteran; the birds are descended directly from the reptiles and became independently adapted to flight. Feathers are shown by their development to be highly developed reptilian scales. The bones of a bird's wing, while showing the type of structure characteristic of a vertebrate forelimb, are markedly different from those of a bat. Why are there no bats with feathers and no birds with batlike wings? Absurd, you say. No, only inconsistent with the principle of evolution.

3. VESTIGIAL ORGANS

Almost every animal and every plant has hidden away somewhere in its anatomy one or more organs which seem to serve no useful purpose but which, nevertheless, continue to be developed generation after generation. The human body is not without its quota of these vestigial organs, the caecum and appendix, the little toe, the coccyx, and in most cases the wisdom teeth. In many rodents, for example the rabbit and porcupine, the caecum is enormous and constitutes an important organ of digestion. Man was, of course, not descended from a rabbit, but undoubtedly in some of his ancestors the caecum and appendix were functionally of importance. The same explanation obviously applies to the little toe, coccyx, and the wisdom teeth.

Vestigial hind limbs occur in the python in the form of two small bones on each side, one representing the ilium and the other the femur. From the distal ends of the femur project two small claws which just show between the scales surrounding the anus. The slug (*Limax*) which is often a pest in greenhouses is a mollusk which appears to be without a shell. There is, however, a small, thin, horny plate, the vestige of a shell, imbedded in the flesh of the dorsal side.

4. COMPARATIVE PHYSIOLOGY

The **physiological processes** in different species of animals can be compared just as their structures can be compared. We have already compared many of these processes in man and the frog, such as digestion, assimilation, excretion, respiration, and so forth. Similar comparisons could be made between other vertebrates and between animals of other groups. Careful studies of certain groups of animals have shown that the relationships which their structural characters indicate are the same as those which are indicated by the degree of similarity between the chemical and physical processes which go on in their bodies.

Certain diseases affect only closely related animals or plants. Thus it has been possible to transmit poliomyelitis or infantile paralysis only to primates (monkeys) and these animals have to be used for experimental work on the disease. Among the plants the wheat rust attacks not only the wheat plant but also oats, barley, rye, and other grasses which, however, all belong to the family Gramineae.

The subject of antibodies was briefly discussed under immunity in the chapter on bacteria and mention was made of precipitins which

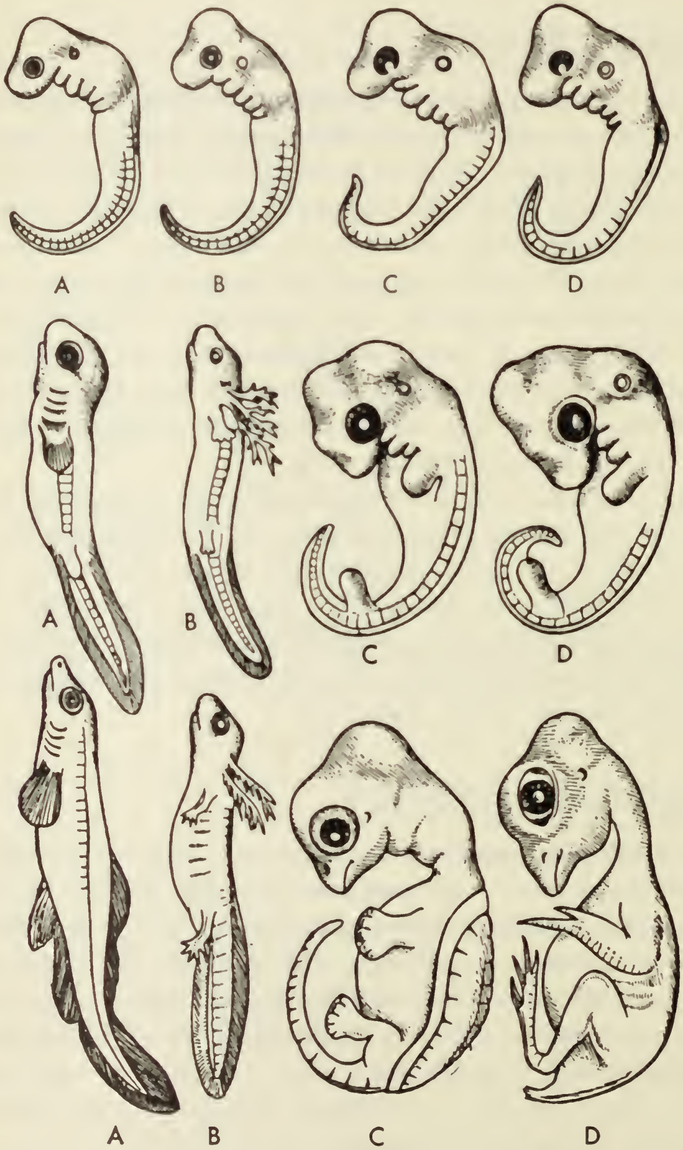

Fig. 42:2 A A series of embryos of lower vertebrates. A, fish; B, salamander; C, tortoise; D, chick. Note the close resemblance between the embryos in the earliest stage (top row) and that the differences become more marked as development proceeds. After Romanes, *Darwin and after Darwin*, from Lindsay, *Evolution and Genetics*, by permission of the Open Court Publishing Company.

immobilize bacteria. Precipitins are formed in the blood not only in response to the presence of bacteria and their products but also when a foreign protein, such as that from the tissues or body fluids of another animal, is injected. Thus, if blood, or better, serum from a dog is injected

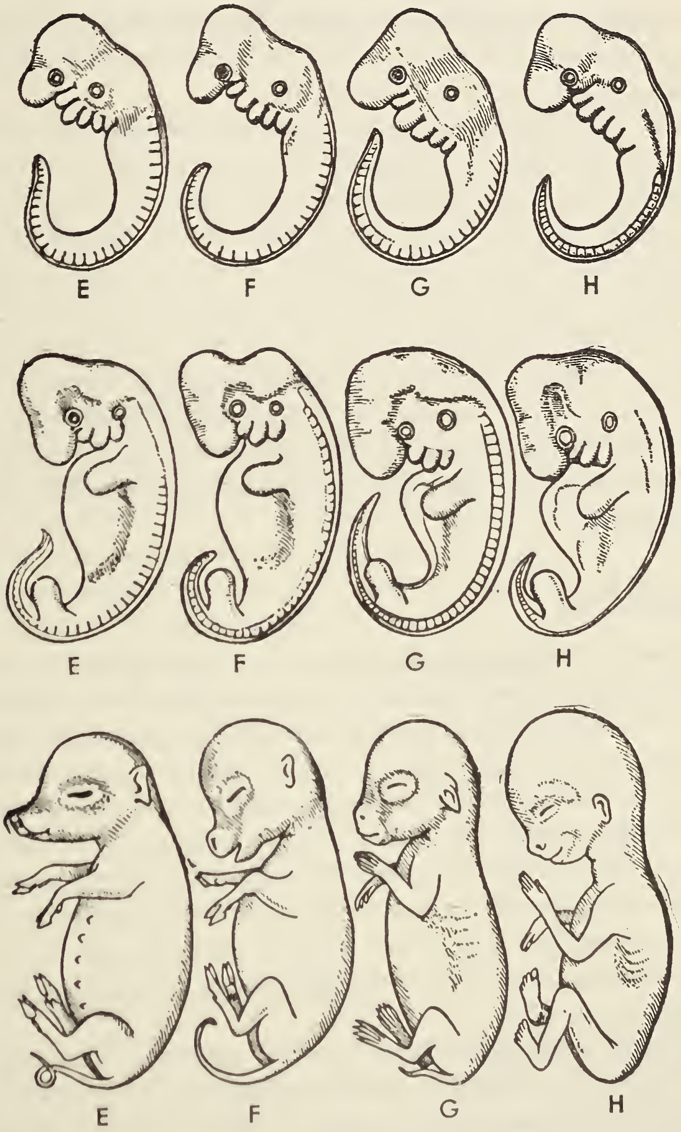

Fig. 42:2 B A series of mammalian embryos. E, pig; F, calf; G, rabbit; H, man. Note that the earliest stages of the embryos resemble those of the lower vertebrates, and that in even the latest stages the embryos resemble each other. After Romanes, *Darwin and after Darwin*, from Lindsay, *Evolution and Genetics*, by permission of the Open Court Publishing Company.

into a rabbit, the blood of the latter will in time develop precipitins, and when the blood of this rabbit is added to the blood serum of a dog, precipitation of proteins will occur. The precipitins developed in the blood depend on the particular kind of foreign protein which is injected. Thus in the above example the precipitins developed in the rabbit's blood in response to the presence of the dog serum are most effective in causing precipitation in dog's serum, and either entirely ineffective or much less so when added to horse serum.

Precipitin tests thus provide a means of studying the relationships between animals from a physiological point of view. "For instance, Nuttall found that when rabbit blood-serum which has been immunized against human blood-serum is mixed with the moderately diluted sera of man, apes, and monkeys, respectively, it reacts with all, though in a varying degree. When mixed with more highly diluted sera from such animals, it forms a precipitate only with man and the manlike apes (chimpanzee, orang-outang, gorilla), the chimpanzee standing nearest to man," [1] and not with the serum from monkeys. Precipitin tests have been applied to other groups of mammals and have served to confirm existing classifications. More recently the method has been applied to amphibians and reptiles.

5. EMBRYOLOGY

The **theory of recapitulation** states that organisms pass through in development stages corresponding to adult stages of organisms lower in the scale of evolution. How does it come about that each individual in its development goes through a series of stages corresponding to the series of stages which classification, comparative anatomy, and comparative physiology indicate as stages which were passed through in the evolution of the species? Why, for example, do gill clefts appear in the embryos of all mammals? Descent with modification would seem to offer the best explanation. Gill clefts develop in mammals because they developed in their ancestors, where they were present not only in the embryo but in the adult.

Comparative embryology offers further evidence. The more nearly animals or plants are related in their classification, comparative anatomy, and comparative physiology, the more do their embryos resemble each other, especially in the early stages. Indeed it is usually only in the later stages of embryonic development that specific differences appear (Fig. 42:2). From the figure it is clear that only an expert would recognize the

[1] Guyer, Michael F., *Animal Biology*, Harper & Brothers, New York, 1937.

differences between the vertebrate embryos illustrated in the first row. Only in the later stages illustrated in the third row can the embryos be distinguished as those of a fish, an amphibian, a reptile, a bird, and four different mammals.

6. DOMESTICATION, CULTIVATION, AND EXPERIMENTAL BREEDING

Many of our most useful plants have been cultivated and our most useful animals domesticated by man since prehistoric times and many changes have been brought about. In certain cases the ancestral form has been found and the relationship of the cultivated varieties traced. For example, the wild cliff cabbage which is still found growing in Europe is known to be the ancestor not only of the cultivated cabbage but of a whole series of plants very different in appearance and put to different uses, including the broccoli, the kale, the kohlrabi, the Brussels sprout, and the cauliflower (Fig. 17:2).

The dog was probably the earliest animal domesticated by man and its origin is therefore in some doubt. By some authorities it is believed to have been descended from a species of wolf now extinct, others would find its ancestor among existing wolves, while still others believe that the different domestic varieties now existing have come from the interbreeding of two or more wild species or races. In any case the number of domestic varieties and the way in which they differ in size from the Newfoundland to the Pekinese and in build from the English bull to the Russian greyhound is amazing. Indeed a dog show resembles in variety a miniature zoological garden. Yet we know that all the canine breeds have arisen under domestication from a single or at most a few very similar wild ancestors. Descent with modification has produced all these varieties during the comparatively short time man has had animals under domestication.

7. GEOGRAPHICAL DISTRIBUTION

Investigation has shown that in most cases the present distribution of species, genera, or even larger groups of plants and animals is best explained by assuming that each has arisen at a certain point on the earth's surface, called a **center of dispersal,** and has spread out to occupy the area it now inhabits. A striking example of this and also one which seems to show evolution at work is found in a certain genus of snails (*Partula*), in the valleys between the mountains of Tahiti. These islands were visited by a naturalist, Garrett, in 1861–1884, and later by another investigator, Crampton, in 1907, 1909, 1919, and 1923. The later surveys showed the spreading of species over new areas and their differentiation into subspecies differing in size, shape, and color. "For example, *Partula clura*, rare in Garrett's time and restricted to a series of valleys comprising only one-fourth the area of Tahiti, had spread over four-fifths of the whole island at the time of Crampton's visits and broken up into seven subspecies. Similarly *Partula modosa* had spread into six other valleys and had originated three new varieties; and *Partula otaheitana* displayed eight subspecies and varieties of varying degrees."

The distribution of animals and plants is much affected by the presence of **barriers.** These are of many kinds and depend on the nature of the habitat of the plant or animal concerned. Thus for a land animal a river, a lake, or an arm of the sea is a barrier; for a fish, land is a barrier. Mountains are barriers for most animals and plants because of the changes in climate which occur as they are ascended. Lack of food or the presence of enemies may constitute barriers. Barriers not only check the spread of species into new areas, but they isolate them from competition with other species. There is evidence that **geographic isolation** is a factor in the production of new species; animals or plants which live in isolation tend to evolve along lines different from the parent stock from which they became separated.

The effect of barriers is seen in the kinds of plants and animals which live on **oceanic islands.** We shall consider in somewhat more detail the case of the Galapagos Islands. These islands are situated on the equator between 500 and 600 miles off the west coast of South America. They were discovered in the early sixteenth century. Darwin visited and explored them in 1835 on his voyage around the world and they have since been visited and explored by a number of scientific expeditions.

"The archipelago is a little world within itself, or rather a satellite attached to America, whence it has derived a few stray colonists, and has received the general character of its indigenous productions. Considering the small size of these islands, we feel the more astonished at the number of their aboriginal beings, and at their confined range. Seeing every height crowned with its crater, and the boundaries of most of the lava-streams still distinct, we are led to believe that within a period, geologically recent, the unbroken ocean was here spread out. Hence, both in space and time, we seem to be brought somewhat near to that great fact — that mystery of mysteries — the first appearance of new beings on this earth." The plants and animals on these islands are clearly the descendants of such forms as could have found their way or been transported by natural agencies to the islands. "Of toads and frogs there are none: I was surprised at this considering how well suited for them the temperate and damp upper woods appeared to be."[1] The explanation is given by Darwin in the *Origin of Species:* "As these animals and their spawn are immediately killed (with the exception, as far as is known, of one Indian species) by sea water, there would be great difficulty in their transportal across the sea, and therefore we can see why they do not exist on strictly oceanic islands. But why on the theory of creation they should not have been created there, it would be very difficult to explain."[2]

The effect of **isolation** in leading to the formation of new species is well shown on oceanic islands. "Although terrestrial mammals do not occur on oceanic islands, aerial mammals do occur on almost every island. New Zealand possesses two bats found nowhere else in the world; Norfolk Island, the Viti Archipelago, the Bonin Islands, The Caroline and Marianas archipelagoes, and Mauritius all possess their peculiar bats. Why, it may be asked, has the supposed creative force produced bats and no other mammals on remote islands? On my view this question can easily be answered; for no terrestrial mammal can be transported across a wide space of sea, but bats can fly across. Bats have been seen wandering by day far over the Atlantic Ocean."[3] Hence we have only to suppose that such wandering species have been modified in their new homes in relation to their new environment. When introduced by man, many groups of mammals thrive in these islands. Rabbits introduced from Europe have become a serious pest in New Zealand. The reptiles of the Galapagos Islands are peculiar. There are few species, but each species is represented by a large number of individuals. The list includes one small lizard belonging to a South American genus, two species of large lizards, one snake identical with a Chilean species, more than one species of sea turtle, and two or three species of land tortoises. The two species of large lizards and the tortoises are especially interesting. One species of lizard is marine, basking on the rocky sea beaches and swimming out to sea to feed on an alga which grows on the sea bottom below tide marks; another is terrestrial, living in burrows and feeding on cactus and the leaves of trees. The tortoises grow to a great size, some so large as to require eight men to lift one from the ground. They occur in great numbers, feed chiefly on cactus, and inhabit the arid parts of the islands.

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[1] Darwin, Charles, *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle round the World,* John Murray, London, 2d ed., 1879.

[2] Darwin, Charles, *The Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life,* John Murray, London, 6th ed., 1880.

[3] *Ibid.*

Darwin remarks that there is no other part of the world where reptiles take the place of herbivorous mammals in so extraordinary a manner; and that the geologist will probably refer back in his mind to the Mesozoic — the Age of Reptiles.

8. PALEONTOLOGY

In Chap. 40, The History of Life on the Earth, the fossil record of the occurrence of plants and animals has been discussed. This record shows that the simplest groups of plants and animals were the first to appear. Thus in the Archeozoic and Proterozoic eras what records we have show only the presence of the simplest of animals and plants. Although many well-preserved fossils from the Early Paleozoic have been found, the record shows the absence of any true vertebrates or of any land plants or animals. The migration toward the land began in the Middle Paleozoic as indicated by fossils of certain fernlike plants and the primitive amphibians called **stegocephalians.** The Late Paleozoic shows the growth of forests of tree ferns, and the advent of reptiles and insects, but no angiosperms, mammals, or birds are known from this era.

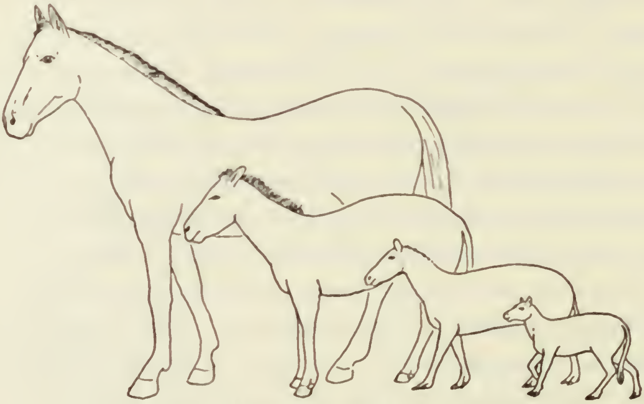

Fig. 42:3 The evolution of the horse.

The Mesozoic, the Age of Reptiles, saw not only the great adaptative radiation of these creatures, but the first flowering plants, mammals, birds, and modern fishes. Lastly, coming to the Cenozoic or Age of Mammals, we find a record of their adaptive radiation and dominance. Only at the end of this era in the Quaternary does man appear upon the scene. Thus the fossil record confirms the evidence of classification, comparative anatomy, comparative physiology, and geographical distribution for the gradual evolution of the higher plants and animals from simpler forms.

The convincing nature of the geological record may best be realized by a careful study of a particular case. The fossil record of the evolution of the horse is probably the most detailed and best preserved of any of the fossil records of plants or animals yet investigated. The horse is distinguished especially by two striking features — its great speed which depends on the special structure and development of its legs, and its ability to exist on the leaves and seeds of grasses which depends in part on the specialization of its teeth for grinding. The earliest known horse

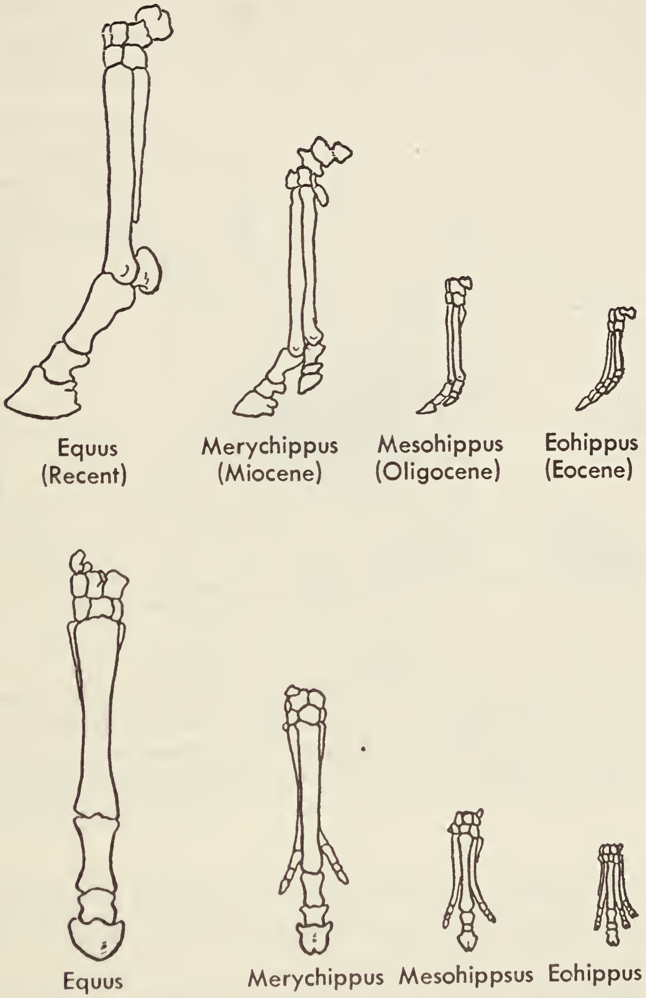

Fig. 42:4 The evolution of the fore leg of the horse. Above, side views; below, front views.

occurred in the early part of the Tertiary Period in the **Eocene** epoch and has been appropriately named ***Eohippus*** (Fig. 42:3). This little creature was about the size of a fox terrier but more slender in the legs and with a longer head. Compared with a modern horse, genus *Equus*, its legs were somewhat shorter. On each of its forefeet it had four toes, corresponding to our four fingers and representing the second to fifth digits of a pentadactyl appendage (Fig. 42:4). On its hind feet it had three toes, numbers two to four. The four toes of the forefeet and the three toes of the hind feet were all placed on the ground and used in walking.

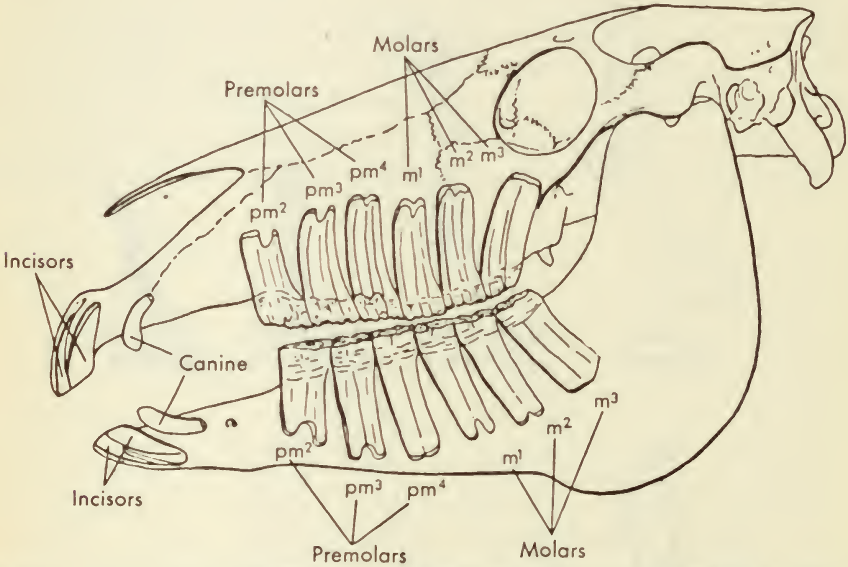

Fig. 42:5 The "dental battery" of an adult horse. pm^2, pm^3, pm^4, second, third, and fourth premolars; m^1, m^2, m^3, first, second, and third molars. The upper first premolars are usually present in the colt as small vestigial nonfunctional teeth. The lower first premolar occurs only very rarely. Note the small canines and the incisors. From Matthew and Chubb, *Evolution of the Horse*, by permission of the American Museum of Natural History.

In the **Oligocene,** the next epoch, a slightly larger fossil horse, ***Mesohippus*,** about the size of a sheep, occurs. In *Mesohippus* there are three toes on each of the fore and hind feet and each toe touches the ground and shares in the support of the weight. In the **Miocene,** which followed the Oligocene, occurred ***Merychippus*,** a horse which reached the size of a small pony. In this horse, although there were three toes on each foot, the middle toes were much the strongest and supported all the weight, the other toes dangling at the side. Other species occurred in the Pliocene and Pleistocene which show further reduction of the side toes. In the modern horse, ***Equus***, the side toes are reduced to the small, scarcely recognizable splint bones which are often fused to the metacarpal or metatarsal of the single supporting digit.

The evolution was, of course, not confined to the legs, all parts of the body of the animal evolved simultaneously in the direction of producing an animal adapted to life on grass-covered plains. While the feet evolved to provide speed in running, the skull and teeth evolved to provide for the grinding of stems and leaves of the coarse, hard grasses which constituted the chief source of food. To this end the jaws lengthened and increased in strength as seen in the lengthening of the whole head (Fig. 42:5). The most conspicuous feature of the teeth of the modern horse is the way in which the premolars and molars are modified for grinding. There are three functional premolars and three molars on each side of each jaw. On account of the way in which the dentine, enamel, and cement are laid down and the unequal wear of these, the grinding surface of the tooth is always maintained rough and uneven (Fig. 42:6). The way in which a horse, and the same is true of a cow, moves its jaws from side to side and back and forth in chewing is familiar. By this movement the rough surfaces of the teeth pass over each other with the grass in between. The gradual evolution of the grinding mechanism of the modern horse can be traced in the fossil horses referred to in the discussion of the evolution of the feet.

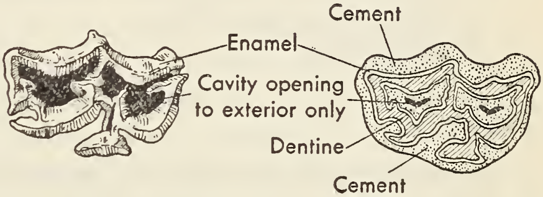

Fig. 42:6 Teeth of the horse. On left, unworn surface of a premolar of a colt before birth showing the upper surface covered with enamel; on right, same premolar after birth showing worn surface which is now composed of cement, enamel, and dentine which have worn away unequally. Clear area, enamel; stippled area, cement; lined area, dentine; solid black, shallow external cavity. Redrawn after Matthew and Chubb, *Evolution of the Horse*, by permission of the American Museum of Natural History.

It should be emphasized that the three fossil forms, *Eohippus*, *Mesohippus*, *Merychippus*, are only a few of the many fossil horses known from the Eocene on. A number of other species showing stages of evolution intermediate between those illustrated are known. On the other hand, not all fossil horses fall into this series. As in the case of other animals, adaptive radiation has also occurred in the horse, so that we see species branching off from the main line of evolution of the modern horse and developing along other lines leading to forms now extinct.

Although Asia and Africa are today the natural homes of all living wild species of the genus *Equus*, and there were no horses in North or

South America when this continent was discovered by the white man, it was mainly in North America that the evolution of the horse occurred. The so-called wild horses of North and South America are feral, being the descendants of domestic horses brought over and allowed to become "wild" by the early colonists.

Topical Outline of Chapter 42

1. Classification 845
2. Homology 847
3. Vestigial organs 849
4. Comparative physiology 849
5. Embryology 850
6. Domestication, cultivation, and experimental breeding 853
7. Geographical distribution 853
8. Paleontology 856

Questions

1. Discuss the meaning of the term "organic evolution."
2. What is meant by the natural classification of plants and animals? Explain how the fact that such a classification can be made is evidence of evolution.
3. What are intergrading species? How does their existence give evidence of evolution?
4. What is homology? What is the natural explanation of the presence of homologous organs?
5. Discuss the evidence for evolution from comparative physiology.
6. Discuss the evidences for evolution from embryology.
7. What evidence of evolution is provided by a dog show or a poultry show?
8. Discuss the evidence for evolution which is obtained by studying the life on oceanic islands.
9. Summarize the paleontological record of life on the earth.
10. Discuss the evolution of the horse. How does it show adaptation?

Suggestions for Further Reading

Lull, Richard Swann, *Organic Evolution*, The Macmillan Company, New York, 1921.

Shimer, Hervey W., *Evolution and Man*, Ginn and Company, Boston, 1929.

CHAPTER 43

The Mechanism of Organic Evolution

1. GENERAL CONSIDERATIONS

Although the idea of evolution as a process of unfolding and development of organic forms dates from the time men first began to think about the relations between the different kinds of plants and animals and how they came to exist upon the earth, the attempt to discover the **mechanism of evolution,** i.e., the exact way in which natural processes combine to bring about the development of new species, really began in the nineteenth century, more than two centuries after the successful application of the scientific method to physical phenomena.

The man who, beyond all others, was responsible for the introduction of the scientific method of observation and deduction into the study of evolution was Charles Darwin. Before considering his work and in order that we may better appreciate what he did we will first consider that of Lamarck.

2. LAMARCK'S THEORY

Lamarck expounded his theory in a speculative work entitled *Philosophie Zoologique* published in 1809. Lamarck's philosophical outlook on life, like that of most of his contemporaries, was vitalistic, i.e., he believed that the organic world as we see it is the result of the action of vital forces different from any of the physical forces which operate in the inorganic world. In the *Philosophie Zoologique* his theory is developed in the form of a series of "laws" which are here called **postulates.**

FIRST POSTULATE. Life, by its own efforts, tends continually to increase the volume of every body which it possesses and to increase the size of its parts up to a limit which life itself determines.

The idea that growth is a characteristic of living matter is stated in an early chapter of this text. Lamarck states it, however, from a vitalistic point of view. We know today that growth is the result of internal and external forces, of the interaction of the organism with its environment.

SECOND POSTULATE. The formation of a new organ in the body of an animal is the result of a new need which has arisen and continues to be felt by the animal and of the new activity which this need initiates and prolongs.

This is directly contrary to the evidence furnished by embryology. For example the vertebrate eye starts to develop in the vertebrate embryo long before there is any need for an eye, and the eye of mammals develops in the darkness of the uterus. How could an unborn animal feel the need of an eye? Further there is no evidence that a mother can transmit the feeling of need to its offspring, especially before the latter has a functional nervous system. Nor is it logical to argue that the evolution of an eye could be brought about by a need of the species because the species is an abstract conception.

THIRD POSTULATE. The extent of development of organs and their power of action is proportional to their use.

This postulate expresses the fact that use tends to increase the development of an organ in an individual and lack of use to degeneration — a fact which no one will dispute.

FOURTH POSTULATE. All changes in or acquisitions to the bodily organization of an individual during its life are transmitted by the process of reproduction to its descendants.

The subject of the inheritance of acquired characters is discussed in the chapter on heredity, and the conclusion is reached that there is no scientific evidence for the inheritance of such characters.

The feature of Lamarck's theory which has received most attention is that relating to the inheritance of acquired characters. This has always had a strong appeal to the popular imagination. It is the fervent desire of every parent that the results of his efforts at self-improvement should be transmitted to his children and to his children's children. The theory also holds out the hope that improving the environment will lead to the improvement of the race. Thus not only will the present generation be made happier, but future generations will benefit. The facts do not support this attractive theory, and it may be doubted whether such a plastic mechanism would in the end lead to any great advances or progressive evolution. The theory of Lamarck fails to give an adequate explanation of the mechanism of evolution because the postulates on which it is based cannot be accepted in the light of present knowledge.

3. DARWIN'S THEORY OF NATURAL SELECTION

Charles Darwin expounded his theory in *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*, published in 1859. Simultaneously and independently Alfred Russel Wallace reached the same conclusions as Darwin, but as Darwin developed the theory in greater detail and after a vast accumulation of facts, the theory is usually associated with his name. As in the case of Lamarck's theory, the theory of natural selection can best be discussed as a series of postulates and conclusions.

FIRST POSTULATE — VARIATION. Individuals of the same species differ and often the differences concern structures important for the individuals.

SECOND POSTULATE — OVERPRODUCTION. In most cases more individuals are born than will survive.

FIRST CONCLUSION — STRUGGLE FOR EXISTENCE. In order to survive an individual must compete with other individuals.

THIRD POSTULATE — THE SURVIVAL OF THE FITTEST. In this competition those individuals which are best adapted to the environment will survive.

FOURTH POSTULATE — INHERITANCE. The fit individuals pass their fitness on to their descendants. This does not imply the inheritance of acquired characters since the fitness may not have been acquired by the individual but may have been due to variation (First Postulate).

SECOND AND FINAL CONCLUSION. **New species** arise by the continued survival and reproduction of the individuals best fitted or adapted to the particular environment.

We may now proceed to consider these postulates and conclusions in more detail. **Variation** is most apparent to us in mankind, especially in men of our own race and in domesticated animals. No doubt the human species is a very variable one and the animals and plants under domestication tend to show great variety. Nevertheless, it must be remembered that most of us are more familiar with the characteristics of man and domestic animals than with those of wild animals. Studies of different species of wild animals and plants have shown that they also are variable and that important differences may occur between the members of the same species. The difficulty is to decide which variations are of survival value, i.e., which variations place the animal or plant at an advantage in the competition for food, protection against enemies, and ability to produce offspring.

The fact that there is an **overproduction** of young individuals must be evident to all. For example a female codfish produces during the breeding season on the average six million eggs which nearly all become fertilized. This means that for every pair of codfish in the sea, six million fertile eggs are laid, and if all of these reached maturity the number of codfish in the sea would be increased three million times each year. As a matter of fact, rather careful records are kept by the governments of countries interested in commercial cod fishing and it is known that although the abundance of the fish varies somewhat from year to year they are probably on the decrease rather than the increase.

It should be emphasized that the **struggle for existence** which Darwin considered such an important factor in evolution does not necessarily imply the idea of a combat between individuals, but merely competition. For example, birds which by strength of wing or skill in maneuvering may have avoided death in a storm may know naught of their weaker fellows who perished.

Darwin's *Origin of Species* appeared six years before Mendel published the results of plant breeding which inaugurated the modern study of **heredity.** The bearing of the present knowledge of heredity on Darwin's theory of natural selection will be discussed in a later section.

On the whole it may be said that the logic of Darwin's reasoning and the army of facts which he brought to support it have withstood eighty years of bitter and violent criticism.

4. DE VRIES'S MUTATION THEORY

In 1886 Hugo de Vries began a long series of experiments on various wild and cultivated plants which led him to propound his "mutation theory" in 1905 in a book entitled *Species and Varieties, Their Origin by Mutation.* Many of De Vries's experiments were conducted on the evening primrose, *Oenothera lamarckiana.* By transplanting wild plants of this species to his garden and breeding them, De Vries obtained many new types which differed to an extent which led him to call them new species. It has been shown that De Vries was somewhat unfortunate in the species which he chose for experimentation and that some of his "new species" were due to the segregation or breeding out of recessive characters present in the germ plasm of the wild type rather than to the occurrence of mutations. Nevertheless, it should be said that it is generally admitted that mutations may form a basis for the action of natural selection in the production of new varieties and possibly new species, and therefore that in this respect the mutation theory of de Vries still stands.

5. SOME SPECIAL THEORIES

Any theory of the mechanism of evolution, which, like that of Charles Darwin, assumes descent with modification as the principle cause of the diversity of plant and animal life, must be chiefly concerned, on the one hand, with variations — how they occur and how they are transmitted — and, on the other hand, with the conditions under which variations are transmitted and what determines which variations are transmitted. A number of theories dealing with one or the other or both of these aspects of the problem of organic evolution have been developed and have had considerable influence on biological thinking.

In the account of the germ-cell cycle in animals in Chap. 37, the primordial germ cells were described as early separating from the somatic cells. This observation coupled with the lack of evidence for the inheritance of acquired characters has led to the development of a **theory of the continuity of the germ plasm** according to which the germ cells are believed to lead a life entirely apart and independent of the soma cells. While this seems to be at least very largely the case in some invertebrates, e.g., the roundworm *Ascaris*, it is apparently not the case in others, where, as in *Hydra*, a part of an animal not containing reproductive organs may regenerate into an entire individual and the regenerated individual may produce germ cells. Although regeneration to this extent is not known in vertebrates the early stages of the germ cells seem to be by no means distinctly separated from the soma cells. In the higher plants a germ-cell cycle in the sense of a clearly separate generation of cells does not seem to exist.

In keeping with the theory of the continuity of the germ plasm is the **theory of germinal selection** advocated by August Weismann (1834–1914). According to this theory selection occurs among the germ cells rather than among the individuals produced by them. There is no evidence that such selection occurs among germ cells. Since the theory does not postulate any relation between the characters selected in the germ cells and the adaptation of the resulting individual, it would not seem to offer any real explanation of evolution.

The **theory of orthogenesis** (Gr. *orthos*, straight + *genesis*, development) has appealed chiefly to paleontologists and is usually attributed to Theodor Eimer (1843–98). According to the theory, evolution has tended to take and pursue certain directions which have in many cases led to overspecialization and to the development of structures beyond their usefulness. Examples cited include the enormous recurved tusks of the extinct mammoths and mastodons (Fig. 40:12), the huge antlers of the extinct "Irish elk," the heavy armor plates and spines of some of the dinosaurs, and the long uncoiled shells of the extinct mollusks known as ammonites. In the earlier forms of the theory the rectilinear development is due to variation occurring in a definite direction. There is no evidence that variation tends, in general, to occur in definite directions. In later forms of the theory selection is given the role of determining the rectilinear development. Selection should tend to act in directions producing definite adaptations. But why the adaptations should develop beyond any possible usefulness, if they do, is not clear.

6. THE ORIGIN OF SPECIES IN THE LIGHT OF PRESENT KNOWLEDGE

A. THE SPECIES CONCEPT

The question "What is a species" was briefly discussed in the section on taxonomy in Chap. 3. There the term species was defined as "a group of organisms which are similar morphologically and physiologically, which normally breed only within the group and which have in common a certain complex of hereditary characters which in general constitute the characteristics of the species." Actually species are usually defined by listing certain characters which serve to distinguish the individuals of the particular species from individuals of other species of the same genus, the genus having been already defined. Thus the eastern gray squirrel, *Sciurus carolinensis*, may be defined as a squirrel of rather large size with a large broad bushy tail equal in length to the body, short legs, rounded head and soft fur, grayish or rusty yellow above, and white underneath. It cannot be denied that some of these characters are rather vague, and if one were confronted with an individual squirrel of unknown species it might be difficult or impossible to determine from this description whether or not it belonged to the species *carolinensis*. Nevertheless a farmer's boy familiar with gray squirrels would have no difficulty in identifying it. For this reason many biologists regard the idea of a species as something more than a mere collection of characters and give to each species a kind of individuality resembling that which is given to particular individuals.

Thus the term **species** has been used for two fundamentally different concepts. According to one of these a species is an abstraction and is defined by a list of characters each of which may vary within a given range. In this case the systematist tries to keep in mind an ideal individual which represents a sort of average for the species. Such an ideal individual is not to be confused with a "type specimen" of a species. This latter is usually the first specimen of the species to be described and is usually kept for reference. According to the other concept, which may be said to be more concrete, a species is a group of individuals which constitute a taxonomic unit. If all the individuals of the species past and present could be collected together they would constitute the species, and any definition of the species would have to be based on the group as a whole. Both concepts are difficult to apply in practice. Thus the abstract concept dealing with an ideal individual is either subject to the personal ideals of each particular investigator or arbitrarily stated by some authority; while the attempt to be concrete leads to a concept involving more individuals than can possibly be observed, at least in most cases. The fact is that most species grade into other similar species. From the point of view of the origin of species and the evolution of organisms in general the more concrete conception of a species as fundamentally consisting of a specific group of individuals has proved the more serviceable.

B. SUBSPECIES AND POPULATIONS

Most species are limited to a definite geographic range outside of which they do not occur and within which they may occur. Studies of large numbers of individuals collected over the geographic range of a species frequently show that the species may be divided into **subspecies,** the individuals of which possess certain characteristics in common not possessed by the other members of the species. Such subspecies usually have a more limited geographic range than the species as a whole.

In the study of species the term **population** is frequently used. A population is a group of individuals inhabiting a given area. A species or a subspecies may include one, several, or many populations inhabiting an area within the area inhabited by the species or subspecies. It is seldom that all the individuals composing a population can be studied. A sample must be chosen. The aim is usually to take a **random sample,** i.e., one in which the individuals have been collected without regard to any particular characters or qualities. Such a sample is then taken as representing the entire population. Obviously this depends on how the sample was chosen and whether it is truly a random sample.

C. VARIATIONS WITHIN SPECIES

Variations within species take two main forms: variations which are not inherited and which are usually attributed to an effect of the environment, and variations which are inherited and are hence due to changes in the hereditary material. Variations which are not inherited are not regarded as playing any direct role in the formation of new species and therefore will not be considered here. Inherited variations are the result of either mutations, i.e., changes in the hereditary material, or to reassortment of the hereditary material already present.

The mutation theory of De Vries is referred to in Sec. 4 of this chapter. As stated there, the plants with which De Vries worked are believed to have been hybrids and the "new species" which he described to have been the result of the reassortment of hereditary characters already present in the parents rather than of mutations. Nevertheless, mutations now are believed to provide the main source of the hereditary differences between species. Although it is probable that the mutations serving to differentiate species may be of any of the types described in Chap. 38, it seems likely that gene-mutations play the chief role.

In considering whether mutations can or cannot provide the raw material for natural selection certain questions arise:

1. **Can the differences actually observed between the individuals of different species be shown to be due to mutations?** Obviously it is not possible, by present methods, to make this determination in all or even a large proportion of the known species; if for no other reason, because most species will not interbreed or if they do interbreed produce sterile hybrids. However, in some cases it has been possible to show that certain of the differences between species depend on hereditary characters which obey Mendel's laws and therefore are regarded as mutations. An example is found in two species of the primrose genus. The flower of the Caucasian primrose, *Primula Juliae*, has a purple pigment in its sap and no pigment in its plastids, while another species, *Primula acaulis*, differs from it in having, among other characters, a yellow pigment in its plastids and no pigment in its sap. When the two species are crossed the hybrid has both pigments. When the hybrid, which is fertile but not so fertile as either of the parent species, is backcrossed to *Primula acaulis*, approximately equal numbers of plants with and without the purple pigment in the sap are obtained, showing that in this case the purple pigment behaves as a simple dominant. When the hybrid is selfed, i.e., fertilized with its own pollen, approximately one in sixteen of the offspring are without either pigment which is what would be expected if the yellow pigment in the plastids also behaves as a simple dominant. Probably only in rare instances is the inheritance of the characters which separate species as simple as in the case indicated. More usually, it would seem,

the characters are due to one or more series of multiple factors. This has been found to be true of the characters which serve to distinguish the wild species of the deer mouse, *Peromyscus*.

2. **Are mutations ever advantageous to the individual and therefore possible steps in evolution?** In many cases it is not possible to determine from observation alone whether a given character is advantageous, indifferent so far as the life and reproduction of the individual, or disadvantageous. It may safely be said that most of the mutations discovered in breeding experiments are obviously disadvantageous to the individual under its normal mode of life. This is well shown in the mutations discovered in *Drosophila*. Nevertheless, a few mutations are known to be advantageous. An example is found in a race of vermilion-eyed *Drosophila* which was able to establish itself in considerable numbers in the wild state in competition with wild type *Drosophila*. Another example is the mutation from single-brooded, i.e., giving one brood in a year, to double-brooded in silkworms. Again the matter is probably seldom so simple as it appears in the above examples. A mutation may be advantageous in one environment and disadvantageous in another. Two mutations each disadvantageous when alone may, when combined, produce a type showing advantages over the wild type. For example, the size of the teeth and the size of the jaws seem to be determined by different genes. Large teeth when inherited with small jaws may become crowded and displaced and thus prove a disadvantage. Small teeth in large jaws are also a disadvantage. However, if large teeth and large jaws are inherited together the result may be advantageous.

3. **Is there a tendency for mutations to occur in certain definite directions** or along certain lines and thus to determine the course of evolution? This would mean that there was something in the nature of the gene or in the process of mutation which limited changes in the gene to those in certain directions only. If this were to have a direct bearing on evolution the limitations would have to be such that successive mutations occurred in such a way as to build up new species of a certain type. This would give support to the theory of orthogenesis referred to in a previous section. Although it seems that individual genes are limited to but a few changes these changes do not seem to occur in general in any particular direction nor in general to follow each other in any particular order although the rate of mutation is different for different mutations. Nor, as already indicated in the previous section, is there any evidence that mutations tend to take the form of adaptations to the environment rather than the reverse.

D. SELECTION

Artificial selection as practiced for centuries by breeders of plants and animals must be distinguished from natural selection, a term used by Darwin for a process which he believed to be operative in the formation of new species in the wild state. In artificial selection in most cases the number of individuals dealt with is necessarily very small compared with the number in a species in the wild state. Also the period of time during which selection has been practiced even in the case of the oldest domesticated animals or plants (five or six thousand years) is extremely short when compared with the geological time available (perhaps a million or more years) for the evolution of a new species in nature. Further, selection as practiced by man has had for its purpose the production of types which either appealed to his particular fancy or were useful to him. Thus the characters which have been selected were not necessarily such as would prove advantageous to the species in a wild state. This has obviously happened in the case of certain breeds of dogs. It is therefore not possible to apply directly the results or conclusions from artificial selection in breeding practice or experiments to a discussion of natural selection.

Some direct observations have been made which seem to show that **natural selection** occurs. The subject of one such set of observations was a common species of crab, *Carcinus maenas*. On a certain shore in England where this crab is abundant a breakwater was constructed which led to an increase in the silt in the water. Measurement of the carapace of crabs caught during a period of years after the building of the breakwater showed that the width of the carapace decreased relatively to the length of the body. Crabs were also placed in aquaria containing silty water and it was found that the individuals which survived had relatively narrower carapaces than those which died. Presumably the narrower carapace was correlated with smaller openings to the gill chambers and this in turn reduced the amount of silt reaching the gills.

A number of observations on different species have shown that individuals with certain characteristics tend to outlive other individuals lacking these characteristics or having them in a greater or lesser degree, but in most cases it has not been possible to show how the particular characters aid or oppose the survival of the individual. However, as will be shown later, the possession of a very slight advantage or disadvantage by certain members of a group of organisms may, in a long time, have a great effect on the proportion of such individuals in the group. Further it seems probable that natural selection may occur as a result of the selection of just such slight advantages or the rejection of slight disadvantages.

Two special cases of natural selection were emphasized by Darwin and have been emphasized by some of his successors. They are sexual selection, and protective resemblance including mimicry. **Sexual selection** has been brought forward as an explanation of the presence of highly colored or otherwise ornate males in certain species especially of birds, tropical fishes, and butterflies. In these species there is internal fertilization, and it is claimed that the females in choosing their mates are influenced by certain characters which thus become incorporated in the species. While this is probably the case where there is a definite courtship routine in which the ornamentation is displayed to the female,

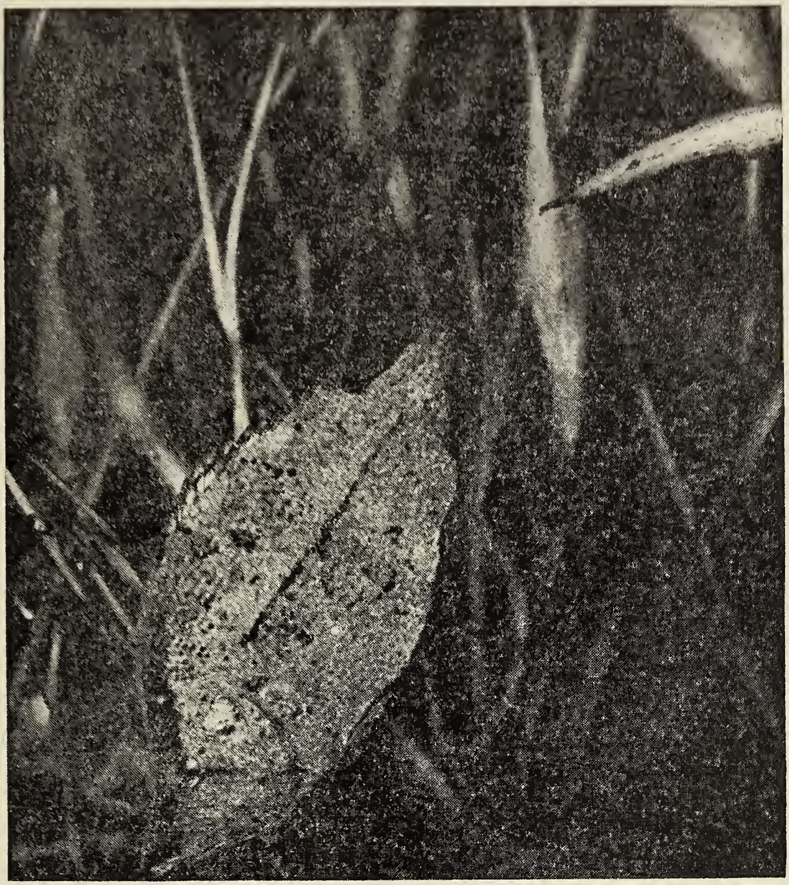

Fig. 43:1 A fresh-water fish, *Monocirrhus polyacanthus*, which seems to imitate a leaf. From a photograph taken by E. G. Boulenger, copyright by the Zoological Society, Regent Park, London, England.

doubt has been cast on those cases in which individual animals, as in the case in many species of birds, claim a particular territory for their feeding operations. In many of these latter cases the ornamentation has been shown to serve as a threat to other individuals of the species attempting to invade another's territory.

Protective coloration and other forms of resemblance to the background (Fig. 43:1) are common in nearly all groups of animals and may possibly occur in plants. It is easy to see the advantage of this to animals which are preyed upon by other animals. Those individuals which are most difficult to recognize will survive. Undoubtedly this offers an explanation of some cases of resemblance.

Mimicry is well seen in certain species of insects where a harmless species may resemble superficially a species which is harmful, because of its sting, nasty taste, or other characters. The harmless species is unmolested because of its resemblance to the harmful species, and it is easy to see how the characters which bring about the resemblance could be the subject of selection. While this may be true in many cases, in other cases the resemblance between the two species may have other causes as, for example, adaptation to similar environments (convergence).

The role which sexual selection and protective resemblance have played or now are playing in the process of evolution can easily be overemphasized. They are at most minor causes of special adaptations.

E. THE STATISTICAL STUDY OF MUTATION AND SELECTION

So far the discussion of the mechanism of mutation has been entirely qualitative. It is obvious that to be convincing such a discussion must be quantitative. For this we turn to statistics.

(1) ALLELOMORPHIC GENES IN A POPULATION, HARDY'S LAW

Let us suppose that two allelomorphic genes, indicated by **A** and **a**, are present in the individuals of a given population. Their existence will lead to the presence in the population of three different genotypes, **AA**, **Aa**, **aa**. The statistical problem is to determine if the proportion in which these different genotypes occur changes from generation to generation in the absence of selection and if so how. We will assume that the genes are not sex-linked so that any gamete may contain either an **A** gene or an **a** gene.

In place of considering the separate individuals of the population we will consider the gametes which produce and take part in the formation of the next generation. From a genetic point of view there will be two kinds of gametes; one kind will contain the gene **A,** the other kind will contain the gene **a.**

Let the number of gametes which contain the **A** gene be x and the number of gametes which contain the **a** gene be y. Then the total number of gametes produced by the population will be $x + y$, and the proportion or fraction of this total number which contain the **A** gene will be $\frac{x}{x+y}$ and the proportion or fraction which contain the **a** gene will be $\frac{y}{x+y}$.

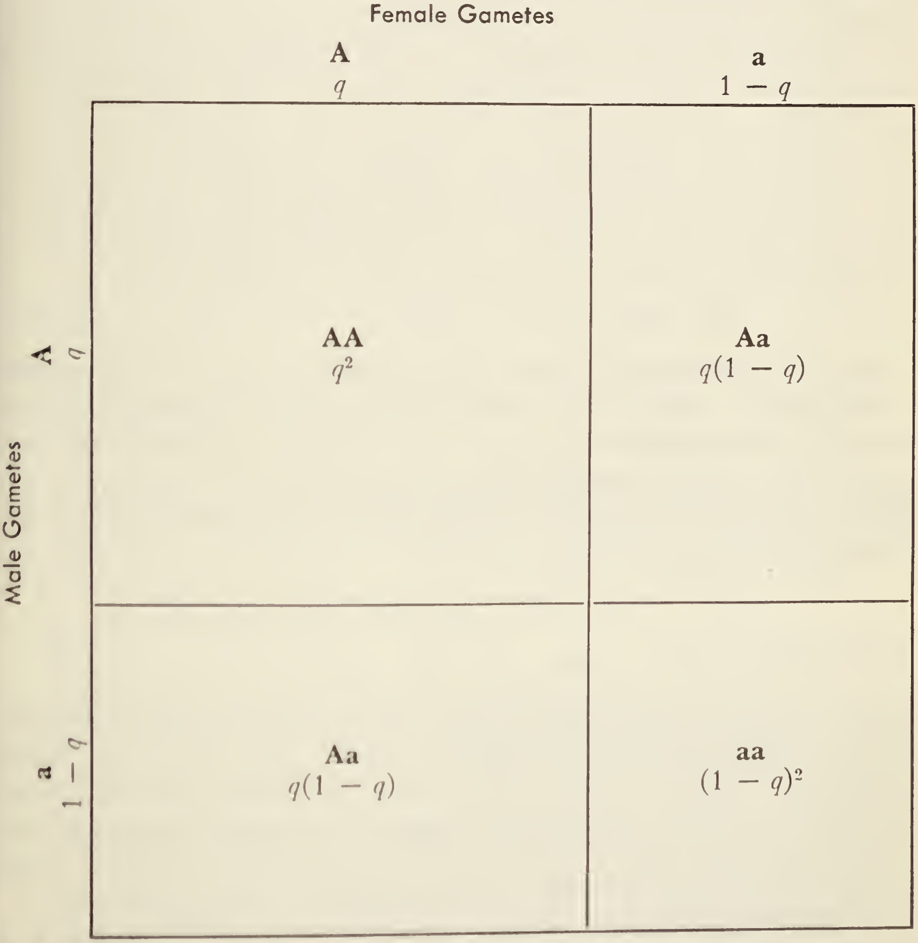

Fig. 43:2 Diagram to show the proportion in which the different types of zygotes are formed in a population in which the allelomorphic genes, **A** and **a**, occur in the proportion **A:a** as $q : 1 - q$. The sides of the rectangles represent the proportions in which the gametes occur. The areas of the rectangles represent the proportions in which the zygotes occur.

It will simplify the calculations if we put $\frac{x}{x+y}$ or the proportion of the gametes which contain the **A** gene equal to q. Then the quantity

$$1 - q = 1 - \frac{x}{x+y} = \frac{x+y-x}{x+y} = \frac{y}{x+y} = \text{the proportion}$$

of the gametes which contain the **a** gene. Thus the proportion in which the two kinds of gametes occur is **A : a** as $q : 1 - q$, where q and $1 - q$ are both fractions and less than one (Table 43:1).

We may now apply to the total population the same kind of reasoning applied to the simple or monohybrid cross in the chapter on heredity (Chapter 36, Section 4, A). The female gametes are **A** and **a** and they are in the proportion **A : a** as $q : 1 - q$. Also the male gametes are **A** and **a** and they are in the same proportion (Fig. 43:2). Any male **A** gamete may fertilize any female gamete. When this occurs the zygotes will be in the proportion **AA : Aa** as $qq : q(1 - q)$. Any male **a** gamete may fertilize any female gamete producing **Aa** and **aa** zygotes in the proportion **Aa : aa** as $q(1 - q) : (1 - q)(1 - q)$. Hence the three kinds of zygotes produced in the F_1 generation are produced in the proportion

$$\mathbf{AA : Aa : aa} \quad \text{as} \quad q^2 : 2q(1-q) : (1-q)^2$$

Since the **AA** zygotes produce only **A** gametes and the **Aa** zygotes produce equal numbers of **A** and **a** gametes, the F_1 zygotes produce **A** gametes in the proportion $q^2 + q(1 - q)$. By similar reasoning the proportion of **a** gametes produced by the F_1 zygotes is $q(1 - q) + (1 - q)^2$. Hence when these F_1 zygotes produce gametes the gametes are in the proportion

$$\mathbf{A : a} \quad \text{as} \quad q^2 + q(1-q) : q(1-q) + (1-q)^2$$

which reduces to **A : a** as $q : 1 - q$

which is exactly the same proportion as that in which they were produced by the previous generation. It therefore follows that when the F_1 zygotes produce an F_2 generation the three types of individuals, **AA**, **Aa**, and **aa** will be in the same proportions as they were in the F_1 generation provided there is no factor, such as mutation or selection, or both acting to change the proportion of functional gametes in each generation.

So far in the discussion we have considered only one generation at a time. A natural population may consist at any one time of several generations. However, it is clear that, under the conditions specified, if the proportions remain constant from generation to generation they will be the same in each generation existing in the population and therefore in

TABLE 43:1. THE PROPORTION IN WHICH GENOTYPES OCCUR IN THE SUCCEEDING GENERATIONS OF A POPULATION IN THE ABSENCE OF SELECTION AND MUTATION

Gametes in population	**A**		**a**	×	**A**		**a**
Proportions in population	q	:	$(1-q)$		q	:	$(1-q)$
Zygotes (F_1) in population	**AA**		**Aa**		**Aa**		**aa**
Proportions	q^2	:	$q(1-q)$	+	$q(1-q)$	:	$(1-q)^2$
which reduces to	q^2	:		$2q(1-q)$		:	$(1-q)^2$
	All		One half		One half		All
Gametes produced by F_1	**A**						**a**
Proportions	$q^2+q(1-q)$			:			$q(1-q)+(1-q)^2$
which reduces to	q^2+q-q^2			:			$(1-q)(q+1-q)$
or	q			:			$(1-q)$

the population as a whole (Table 43:1). Hence it may be said that in the absence of mutation and selection the generic composition of a population remains the same. This is referred to as **Hardy's Law.**

(2) MUTATIONS IN A POPULATION

The frequency of the occurrence of a particular gene or other hereditary factor may be changed by mutation. This is represented by a change in the value of q used in the previous section. Assume, for example, that the mutation is from **A** to **a**, and out of every 1,000,000 **A** genes one mutates to an **a** gene. The **mutation rate** would be $\frac{1}{10^6} = .000001$. In the general case the mutation rate may be indicated by U. The frequency of the **A** gene will then change from q to $(1-U)q$ in each generation. If there is no mutation in the reverse direction, i.e., from **a** to **A**, the **A** gene will eventually be lost and the population will come to be homozygous. Usually, however, mutation occurs also in the reverse direction. Assume that the rate of this reverse mutation, i.e., **a** to **A**, is V.

Then the change in frequency of the **A** gene due to this mutation will be $+V(1-q)$. The change due to the direct mutation, **A** to **a**, is $-Uq$. Hence the total change in the frequency of the **A** gene due to direct and reverse mutation is $-Uq+V(1-q)$. If this quantity is equal to zero the two mutations, direct and reverse, acting together will produce no total change in the population. That is when

$$-Uq+V(1-q)=0$$

or

$$-(U+V)q+V=0$$

or when

$$q=\frac{V}{U+V}$$

Suppose for example, $U=.000001$ or 10^{-6} and $V=.0000005$ or 5×10^{-7}, then the population will be in equilibrium when

$$q=\frac{5\times10^{-7}}{10^{-6}+5\times10^{-7}}=\frac{5}{15}=\frac{1}{3}$$

or when $\frac{1}{3}$ are **A** genes and $\frac{2}{3}$ are **a** genes or when the genes in the population are in the proportion **A** : **a** as 1 : 2. Further the discussion in the previous section has shown that once the genes occur in this proportion their proportion in the population will remain unchanged and the mutations will have no further effect, provided always that the mutation rates do not change and that there is no selection of individuals of one genotype in preference to those of another.

Except in a few special cases and under special conditions not usually found in nature the rate of mutation is exceedingly slow, of the order of 10^{-5} to 10^{-6}, and not very different in different organisms. In corn, an angiosperm plant, *Drosophila*, an insect, and in man and other mammals most mutations seem to occur in approximately the same order of frequency although some differences do occur.

Thus when a mutation is indifferent to the species, i.e., neither advantageous nor disadvantageous to the individual, it tends to accumulate in the population until a certain frequency is reached, after which the frequency in which it occurs remains constant. In this way, provided conditions are such as to keep them indifferent, numerous mutations may remain in a population waiting, as it were, the time when conditions may make them advantageous or disadvantageous. When this time occurs selection begins to operate.

(3) SELECTION IN A POPULATION

When selection operates in a population the statistical problem is complicated by the fact that interest is usually centered in the zygote rather than the gametes and in the phenotypes rather than the genotypes since it is primarily on the phenotypes that selection acts. It will be simpler to consider first the case of genic selection where there is a difference in the survival between two allelomorphic genes. Assume that the allelomorphs **A** and **a** tend to survive in each generation in the ratio $1 : 1 - S$, where S, called the **selection coefficient,** is a measure of the selection, being positive and less than 1 when **A** survives in excess of **a** and negative when **a** survives in excess of **A**. For example, if for every 100 **A**-gametes, only 99 **a**-gametes survive, S will be equal to 0.01. Assume now a population in which the **A** and **a** genes occur in the proportion $q : 1 - q$. When reproduction occurs the surviving gametes may be represented by q and $(1 - S)(1 - q)$. For comparison the quantities in this proportion may be divided by the total number of gametes $q + (1 - S)(1 - q) = 1 - S(1 - q)$. It is then evident that the new proportion in which the surviving gametes occur is

$$\mathbf{A} : \mathbf{a} \text{ as } \frac{q}{1 - S(1 - q)} : \frac{(1 - S)(1 - q)}{1 - S(1 - q)}$$

The change in the frequency of the gene **A** in one generation is therefore

$$\text{from } q \text{ to } \frac{q}{1 - S(1 - q)} \text{ or } \frac{q}{1 - S(1 - q)} - q \text{ or } \frac{Sq(1 - q)}{1 - S(1 - q)}$$

When the selection coefficient, S, is small the quantity $1 - S(1 - q)$ in the denominator may be taken as equal to 1, in which case

$$\frac{Sq(1 - q)}{1 - S(1 - q)} \text{ becomes } Sq(1 - q)$$

or the change in the frequency of the gene **A** per generation is equal to the selection coefficient × frequency of gene **A** × frequency of gene **a**.

The discussion may be extended to include selection of zygotes. The three zygotes may be assumed to reproduce in the ratio

$$\begin{array}{ccccc} \mathbf{AA} & : & \mathbf{Aa} & : & \mathbf{aa} \\ 1 & : & (1 - hS') & : & (1 - S') \end{array}$$

where S' is a selection coefficient representing the selection of the **aa** zygote, and hS' represents the survival of the **Aa** zygote. Without going into the mathematics involved in this case, it may be stated that under zygotic selection the rate of increase of the frequency of the gene **A** is

$$S'q(1 - q)[1 - q + h(2q - 1)]$$

In the special case where **A** is completely dominant and the survival of the heterozygote **Aa** is equal to that of the homozygote **AA,** $hS' = 0$ and therefore $h = 0$ in the formula above and the rate of increase of q the frequency of the **A** gene becomes

$$S'q(1 - q)^2.$$

When q is a small quantity $1 - q = 1$ approximately and the formula becomes $S'q$, or when q is small, rate of increase of q is equal to selection coefficient of **aa** zygotes × frequency of **AA** zygotes.

Suppose, for example, that we are dealing with a completely dominant gene, and that $S' = 0.001$ or 10^{-3} and that $q = 0.000001$ or 10^{-6}. Then in the next generation the increase in q is $S'q$ or $10^{-3} \times 10^{-6}$ or 10^{-9}, which means that in this one generation q increases from 0.000001 to 0.000001001. Thus it would take approximately 1000 generations (more exactly 1739) for q to increase from 0.000001 to 0.000002. In the case of a recessive gene the number of generations required to produce the same increase would be approximately 300,000 (more exactly 321,444). However as the value of q is increased progress becomes more rapid until q approaches one half or 50 per cent when it is again slow as shown in the following table:

TABLE 43:2. NUMBER OF GENERATIONS REQUIRED TO INCREASE THE FREQUENCY OF A DOMINANT GENE BY SELECTION WHEN THE COEFFICIENT OF ZYGOTIC SELECTION IS 0.001 [1]

Increase of frequency of dominant gene in per cent of population	0.001 to 1%	1 to 50%	50 to 99%	99 to 99.999%
Generations to produce increase	6,920	4,819	11,664	309,780

F. ISOLATION

The early students of evolution were quick to discover that peculiar species occurred in isolated areas and to conclude that isolation was a factor in the development of new species. By lessening competition isolation may provide an opportunity for mutations not especially advantageous to survive. It would appear that it is more in this capacity that isolation acts. Some isolation seems to be of assistance in the development of new species, especially in their incipiency. It is said that evolution is most rapid in large species divided into partially isolated groups. The isolation favors the survival of diverse mutations which through crosses between the groups may become available to the entire species.

G. THE PRODUCTION OF NEW SPECIES BY MUTATION AND SELECTION

We are now in a position to consider the possible origin of species from the combined effects of mutation and selection. The statistical methods outlined in the previous section can be extended to cover cases involving a combination of mutation and selection but their development would lead us beyond the scope of this text. However, some of the general results can be discussed.

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[1] From Dobzhansky, T., *Genetics and the Origin of Species*, Columbia University Press, New York, 1937.

As already shown, a mutation even though exceedingly rare may, if neutral and not opposed by a more frequent or equally frequent reverse mutation, establish itself in a population. Since it has been assumed to be neutral, this is true whether the mutation is dominant or recessive. Thus in any population there may be accumulated a number of neutral mutations, any one or more of which may become advantageous or disadvantageous depending on conditions.

When a mutation confers an advantage on the individual, selection becomes operative. As shown, even a slight advantage, given time, may lead to the mutation replacing its allelomorph in a large proportion of the population. The same argument applies to a group of genes when most or all of them behave as a unit, i.e., genes linked in the same chromosome. This process of replacement will usually be very slow in the beginning but becomes more rapid as the mutation becomes established.

The question arises whether the process as outlined above, although in most cases exceedingly slow, nevertheless can produce in comparable times changes comparable to those indicated by the geological record. The best information available on the rate of evolutionary change of genera is probably that obtained from the study of the various genera and species of horses from the primitive *Eohippus* to the modern *Equus*, outlined in a previous chapter. But even in this case it must be admitted that any attempt at a determination of the quantities concerned involves many untested assumptions. In the direct line from *Eohippus* to *Equus* there probably occurred eight successive genera. The total time involved is about 45,000,000 years. During this time there must have been at least 15,000,000 generations. A conservative estimate of the number of breeding individuals in the inhabited area is 100,000. Thus a total of at least 15,000,000,000,000 or 15×10^{12} individuals were actually or potentially concerned in this ancestry of *Equus*. A mutation rate of .000001 for any particular gene would result in the production of 1,500,000 mutations of that particular gene. If the somewhat plausible assumption be made that one-fifth of these mutations were advantageous, we have a total of 300,000 advantageous mutations which may become established by natural selection. Many of these mutations will be identical. Assume that one in every thousand gives rise to an evolutionary change. Then we arrive at 300 structural steps in the evolutionary series from *Eohippus* to *Equus*. Consider for example that we are dealing with steps in the evolution of the *Equus* tooth, more particularly its increase in the length as measured along its lateral face. This length in *Eohippus* is on the average about 8 millimeters and in *Equus* about 40 millimeters or an increase of about 32 millimeters. If this increase were divided into 300 steps, each step would represent an increase of 0.1 millimeter, an amount which is much less than the variations found in specimens of the same species.

It therefore appears mutations causing extremely small differences in individuals and occurring at rates such as those observed in laboratory experiments could provide material for evolution at a rate equal to or even greater than that which occurred in the evolution of the horse.

7. SOME GENERAL CONSIDERATIONS

It should be emphasized that the process of evolution is a very complicated one, infinitely more complicated than the simplifications necessitated by an elementary outline would indicate. Not only is the origin of each species usually the result of a multitude of small changes, many times reassorted and delicately adjusted to the organism as a whole, but the origin of larger divisions must be proportionately more complex. Through it all the actual changes seem to occur at random, and only by a sort of trial and error do they become established. Attempts to visualize the process in a so-called tree of life or in lines of descent fail to give a full picture and are often misleading. Rather than resembling a tree the descent and modification of organisms resembles a fine irregular network spread out in all directions and showing a coarser pattern in which separate species, genera, and higher divisions may appear and disappear. Looked at in a cross section representing an instant in the long course of geological time each form seems fixed and permanently arranged, but seen in perspective all is changing and no form remains permanent.

The thoughtful student will also ask whether random mutation, and isolation and natural selection which seem sufficient to cause species to change and new species to arise, are also able to bring about those major changes which have produced the different phyla and whether any process depending on random mutations could have built up organisms as complicated as the higher plants and animals. At present no satisfactory direct answer can be given. That long eons of time and billions of individuals are involved is not in itself an entirely satisfactory answer.

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Questions

1. Explain clearly the difference between a proof of the occurrence of evolution and an explanation of the mechanism of evolution.
2. Why is Lamarck's theory untenable?
3. State the postulates and conclusions of Darwin's theory of natural selection.
4. Why is Darwin's theory of natural selection generally accepted today as a factor in the production of new species?
5. Discuss De Vries's mutation theory.
6. Show that in the absence of mutation and selection the genetic constitution of a population remains the same.

Suggestions for Further Reading

Darwin, Charles, *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*, John Murray, London, 1859.

Haldane, J. B. S., *The Causes of Evolution*, Longmans, Green & Company, New York, 1932.

CHAPTER 44

Early Man

1. THE ZOOLOGICAL POSITION OF MAN

The detailed description of the human body and its comparison with that of the frog must have already convinced the student that man has all the characteristics of an animal and should find a place in zoological classification. Man has already been placed among the placental mammals in the order Primates. The discussion of his more exact zoological position has been postponed to this chapter. The order Primates is placed among the Eutheria near the Carnivora to which they probably show the closest relationship rather than at the end of the classification because, except for the cerebral cortex, the Primates are a relatively primitive and generalized order. Anatomical specialization in mammals has tended to affect particularly the limbs, including the feet, and the skull, including the teeth. The limbs have been modified in response to the requirements of locomotion, the skull and teeth in adaptation to feeding. The limbs and teeth of primates show primitive characters. Both fore and hind limbs have five digits which is the primitive number found in amphibians and reptiles. There is a complete set of fairly numerous teeth, none of which is highly specialized.

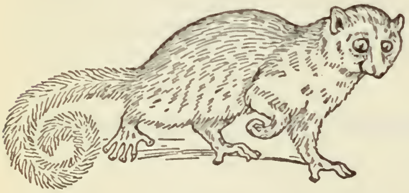


Fig. 44:1 Smith's dwarf lemur (*Microcebus smithi*, suborder Lemuroidea). After Beddard, from Newman, *Vertebrate Zoology*, The Macmillan Company.

The order Primates is divided into three suborders: the Lemuroidea, the Tarsoidea, and the Anthropoidea. The suborder **Lemuroidea** (Lem′u-roi′de-a, L. *lemur*, a ghost) includes the lemurs (Fig. 44:1), small furry arboreal animals with long tails, in appearance somewhat intermediate between a squirrel and a monkey. Lemurs are most abundant in Madagascar but are also found in tropical Africa and some of the islands of the East Indies. They are nocturnal animals and some of them have a curious ghostlike appearance.

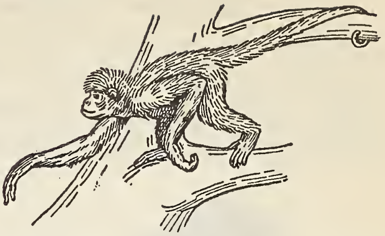


Fig. 44:2 Spider monkey (*Ateles aler*, suborder Anthropoidea, group Platyrrhini, family Cebidae). After Beddard, from Newman, *Vertebrate Zoology*, The Macmillan Company.

The suborder **Anthropoidea** (An′-thro-poi′de-a, Gr. *anthropos*, man + *eidos*, like) includes all the different kinds of monkeys and apes. They are more highly organized than the lemurs. The suborder is divided into two groups, the Platyrrhini and the Catarrhini. The **Platyrrhini** (Plat′yr-rhi′ni, Gr. *platus*, broad + *ris*, *rinos*, nose) are the New World monkeys of South and Central America. These monkeys possess flat noses with the nostrils directed forward, long prehensile tails, and small thumbs (Fig. 44:2). Two families are included in the Platyrrhini: the Cebidae, which include the capuchin monkeys (commonly seen associated with hand organs) and the spider monkey (Fig. 44:2) and the Hapalidae, which include the marmosets (small monkeys about the size of large squirrels, frequently kept as pets).

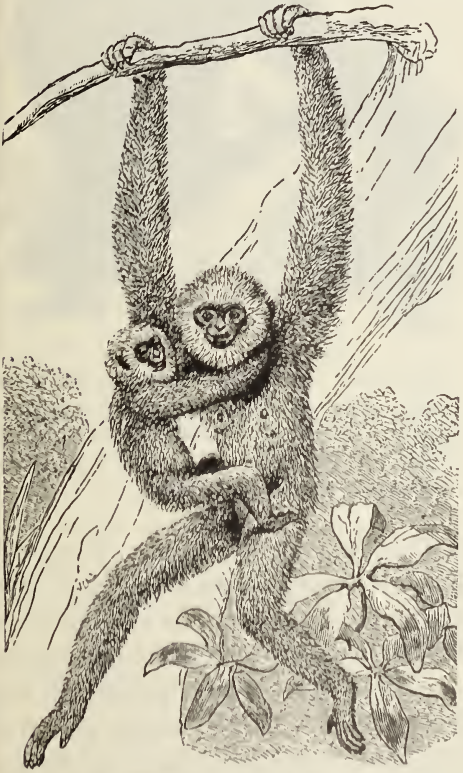


Fig. 44:3 The dun-colored gibbon (*Hylobates entelloides*, suborder Anthropoidea, group Catarrhini, family Simiidae). From Flower and Lydecker, *Mammals Living and Extinct*, by permission of A. and C. Black.

The **Catarrhini** (Cat′ar-rhi-ni, Gr. *cata*, down + *ris*, *rinos*, nose) are the Old World monkeys and apes. In them the nose is curved and the nostrils are directed downward. The tail when present is not prehensile, and the thumb is well developed and opposable. The Catarrhini are divided into three families: the Cercopithecidae, which include baboons, mandrills, and macaques; the Simiidae, which include the anthropoid apes; and the Hominidae, which include man.

In the **Simiidae** (Si-mī′i-dae, L. *simia*, an ape) the tail is absent and the arms are longer than the legs. The **gibbons** (Fig. 44:3) are the smallest and most primitive. The arms are of such a length that they reach the ground when the animal walks upright, which, however, happens only occasionally since these creatures live most of their lives in trees, using their long arms to swing from branch to branch. They are omnivorous but feed chiefly on fruits. The **orangutang** (Fig. 44:4) is a rather heavily built stocky ape with relatively long arms like the gibbons. It lives in trees and builds a crude nest by arranging broken branches in a crotch. When walking it uses its forelimbs and places its knuckles on the ground. Its diet consists exclusively of fruits. The **chimpanzee** and the **gorilla** are man's nearest relatives. The chimpanzee (Fig. 26:15) is a tree dweller but is also at home upon the ground, while the gorilla (Fig. 44:5) is a ground dweller and takes but seldom to trees. In the chimpanzee and gorilla the arms are relatively shorter than in the gibbons and the orang. In general, the first named is less specialized

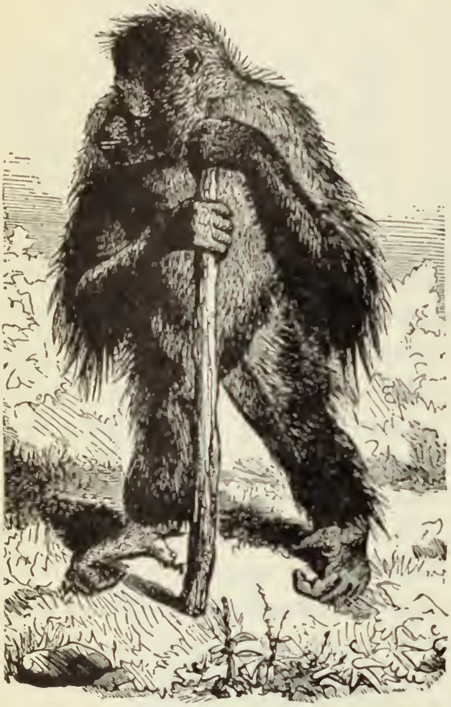


Fig. 44:4 The orangutang (*Simia* or *Pongo satyrus*, suborder Anthropoidea, group Catarrhini, family Simiidae). From Flower and Lydecker, *Mammals Living and Extinct*, by permission of A. and C. Black.

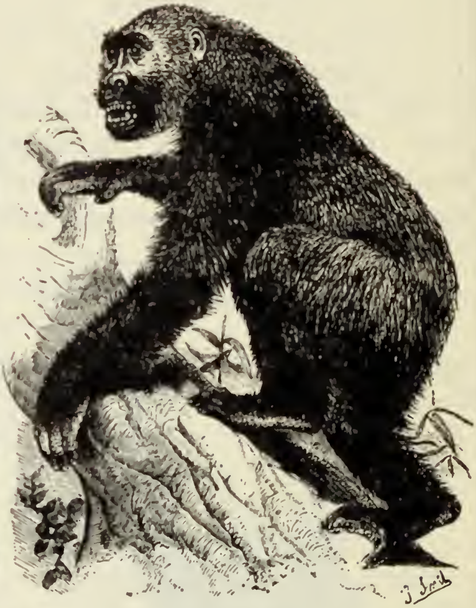


Fig. 44:5 The gorilla (*Gorilla gorilla*, suborder Anthropoidea, group Catarrhini, family Simiidae). From Flower and Lydecker, *Mammals Living and Extinct*, by permission of A. and C. Black.

for an arboreal life. The brain is comparatively well developed and the animal appears to show the beginnings of the human type of mentality.

The family **Hominidae** (Ho-min′i-dae, L. *homo*, *hominis*, man) includes the single living species, *Homo sapiens* (L. *sapere*, to know). Man differs anatomically from the anthropoid apes chiefly in his adaptations to life on the ground and his larger brain. Life on the ground in this case has involved the adoption of the erect posture and walking on the hind legs only. The truly erect posture has brought about modifications in the head, trunk, and limbs. The head becomes balanced on top of the neck, the spine curved, the hips broadened to support the body and the foot elongated and arched. The hands have replaced the jaws in defense

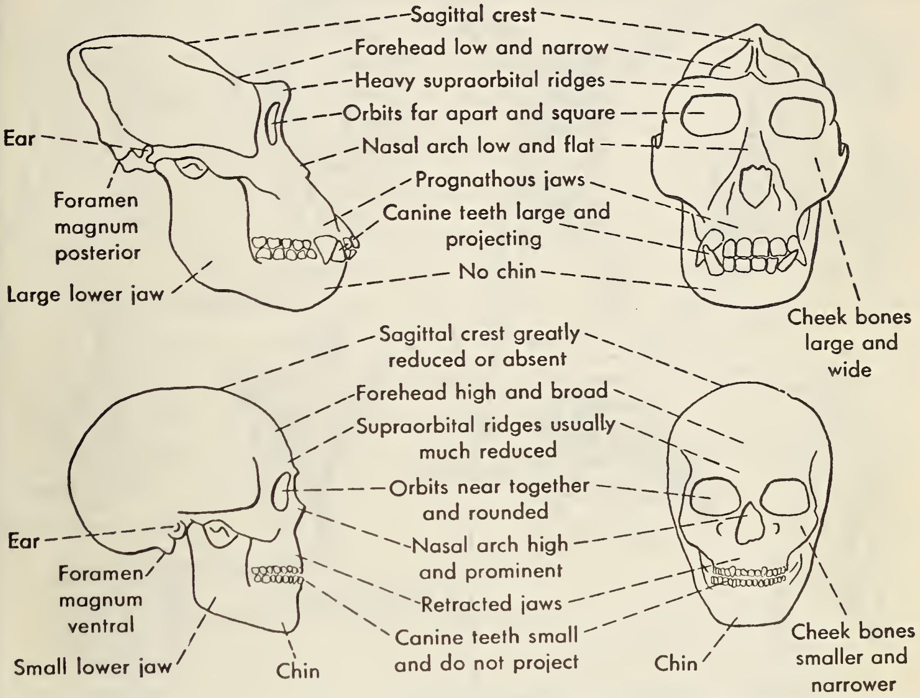

Sagittal crest
Forehead low and narrow
Heavy supraorbital ridges
Orbits far apart and square
Ear
Nasal arch low and flat
Prognathous jaws
Foramen magnum posterior
Canine teeth large and projecting
No chin
Large lower jaw
Cheek bones large and wide
Sagittal crest greatly reduced or absent
Forehead high and broad
Supraorbital ridges usually much reduced
Orbits near together and rounded
Ear
Nasal arch high and prominent
Foramen magnum ventral
Retracted jaws
Canine teeth small and do not project
Small lower jaw
Chin
Chin
Cheek bones smaller and narrower

Fig. 44:6 Diagrams comparing the skull of a gorilla with that of a man.

TABLE 44:1. A COMPARISON OF THE STRUCTURAL FEATURES OF THE ANTHROPOID APES AND MAN

ANTHROPOID APES (FAMILY SIMIIDAE)	MAN (*Homo sapiens*) (FAMILY HOMINIDAE)
Cranial capacity under 600 cu cm	Cranial capacity average, 1400–1500 cu cm
Jaws large and project forward	Jaws smaller than in apes and not projecting, making face nearly vertical
No chin	Chin
Spinal column in a single arch	Spinal column has four distinct curves
Arms longer than legs	Legs longer than arms
Big toe can oppose other digits	Big toe not opposable

and offense. By most authorities all of the different living races of men are regarded as belonging to one and the same species. As we shall see later there previously existed other species of the genus *Homo* and other genera of the family Hominidae.

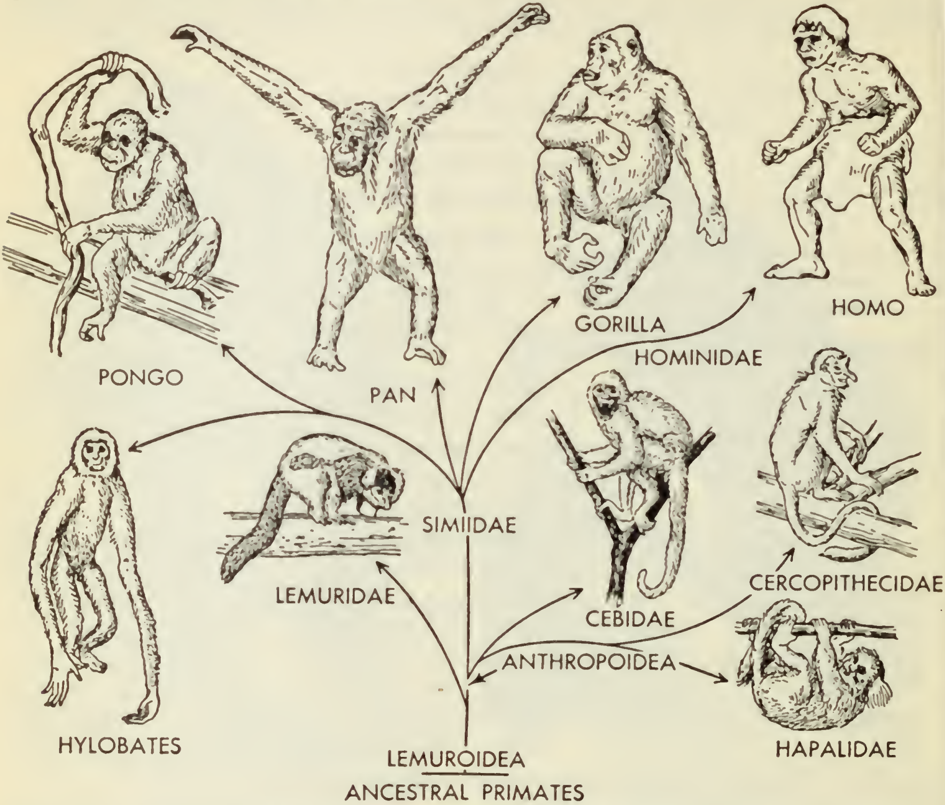


Fig. 44:7 The relationships of the primates. The lines suggest possible relationships. The figures are not drawn to scale. From Hegner, *College Zoology*, The Macmillan Company.

The classification of man discussed in the text is shown below:

- Phylum Chordata
    - Subphylum Vertebrata
        - Class Mammalia
            - Subclass Eutheria
                - Order Primates
                    - Suborder Anthropoidea
                        - Group Catarrhini
                            - Family Hominidae
                                - Genus *Homo*
                                    - Species *sapiens*

In Table 44:1 and Fig. 44:6 the structural characteristics of the anthropoid apes are compared with those of the living species of man.

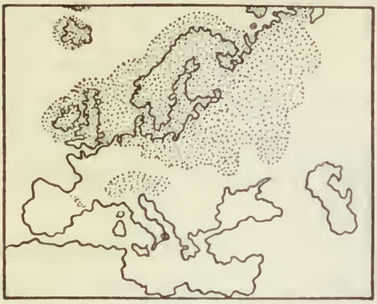
There is little doubt that man and the anthropoid apes had a common ancestor, although there is considerable difference in opinion as to how far back in the genealogical tree of the primates that ancestor is to be sought (Fig. 44:7). One theory (1) regards the family Hominidae as closely related to the anthropoid apes; a second (2) developed by Darwin and Haecker, considers them to be descended from the catarrhine or long-nosed monkeys; a third (3) relates them to the more primitive platyrrhine or flat-nosed monkeys; and a fourth (4) would make their nearest relatives the lemurs, most primitive of living Primates.

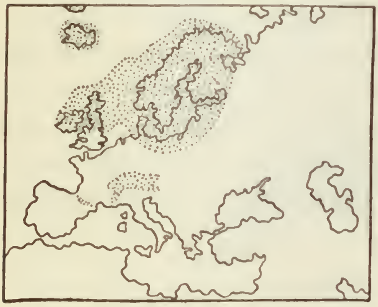
Various parts of the world have been given by different authorities the distinction of being the "cradle of the human race," but there seems little doubt that it must be sought in the Old World and most probably in some part of southern Asia or perhaps Mongolia. From some such center occurred the adaptive radiation of the primitive members of the family Hominidae to the "ends of the earth." The evidence seems to show that this adaptive radiation was already far advanced before the earliest records of human existence at present known were deposited in the rocks. As we shall see in a later section the earliest evidences of man are widely scattered over the Old World.

2. FOSSIL PRIMATES

Unfortunately for the study of the origin of man the fossil record of the Primates is a meager one. This is not surprising when one considers that the existing Primates, and undoubtedly also those of the past, lived in forests and rocky country under conditions which were particularly unfavorable to the preservation of fossils. Although the human family undoubtedly arose in the Old World and did not reach the New World until comparatively late in its history, the Primates as a group probably arose on the American continent, since the earliest known fossil primates occur in the Lower Eocene of western North America. The Middle Eocene of the United States shows a great increase in the numbers and differentiation of these early primates and apparently at about this time primates migrated from North to South America and from the New to the Old World, since their fossils are absent from the later deposits in the United States and first appear in Middle Eocene deposits in France and Switzerland.

From Europe the primates moved into Asia and Africa in the Late Eocene or Early Oligocene and began to differentiate into the various groups of Old World monkeys and apes. A country to the west of northern Egypt, known as Fayum, now a barren desert, has been a fertile source of primate fossils. Three species of monkeys, probably closely related to the ancestors of the anthropoid apes, have been found there in Oligocene deposits. Miocene deposits in the south of France, Germany, Greece, and northern India have yielded various species of fossil monkeys, some of which are classified as anthropoid apes and are believed by some authorities to be closely related to the line of human descent. One of these, *Australopthecus*, from South Africa and probably to be assigned to the Pleistocene, is known by an almost complete skull of a young individual. The skull is that of a higher anthropoid and although the individual was too young to show adult characters these probably included a higher forehead, a shorter face, and more human teeth than either the chimpanzee or the gorilla (Fig. 44:10).


Second Glacial Stage


Third Glacial Stage

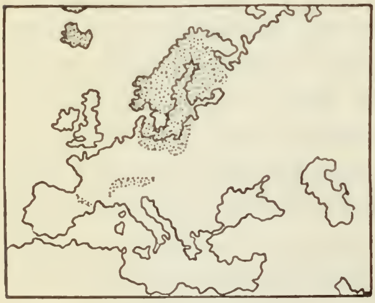

Fourth Glacial Stage

Fig. 44:8 Europe during the second, third, and fourth glacial stages. Dotted areas represent portion under ice cap. After H. F. Osborn, *Men of the Old Stone Age*, by permission of Charles Scribner's Sons.

3. THE GEOLOGICAL HISTORY OF MAN

A. THE NATURE OF THE RECORD

Prehistoric man has left an extensive and interesting record. This record consists not only of his bones and in many cases complete skeletons, but also of many of the things he used and worked upon in his daily life. The term "fossil" is usually applied only to prehistoric remains, and would not be applied for example to the petrified bodies of men and animals buried in the Roman city of Pompeii at the time of the famous eruption of Vesuvius (A.D. 79).

As already described in Chap. 40, The History of Life on the Earth, the Pleistocene consisted of four ice ages or glacial stages separated by three interglacial stages. Much of our knowledge of Pleistocene man has been obtained from European deposits and the dating of these deposits

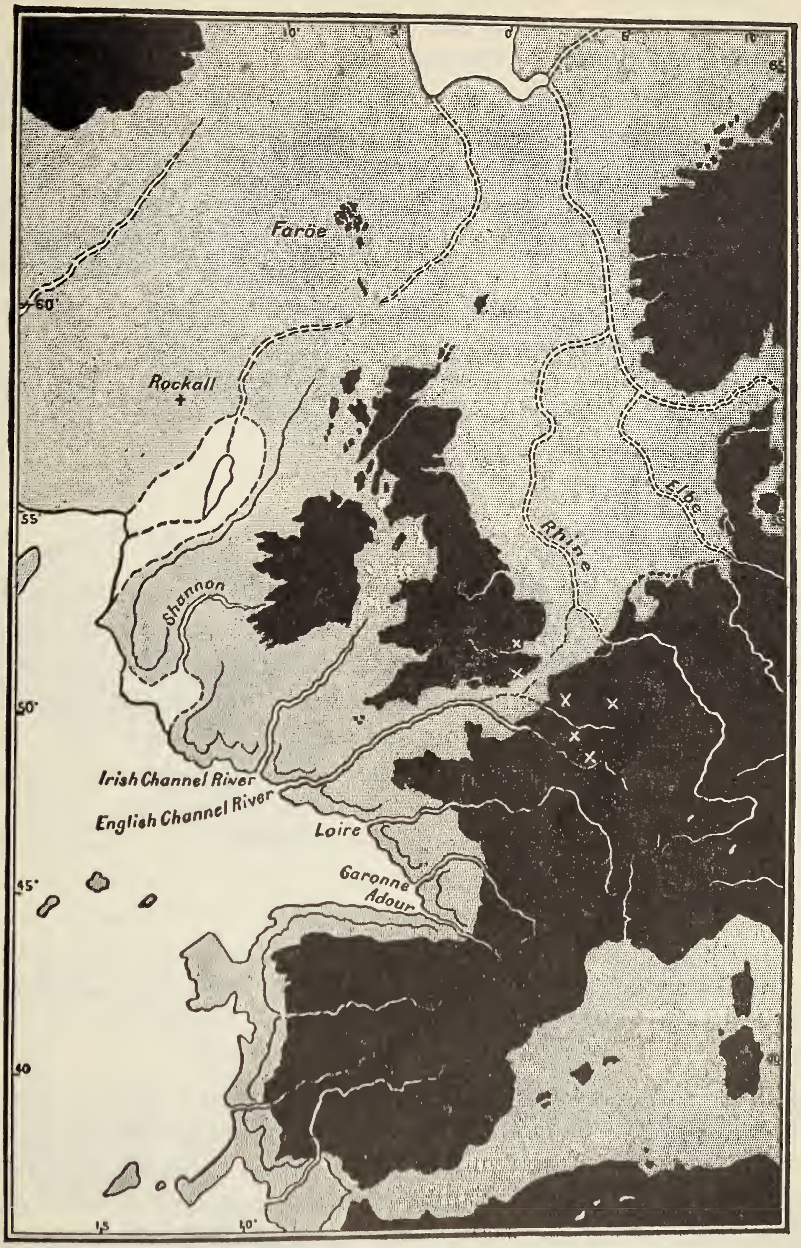


Fig. 44:9 Restoration of Western Europe during the third Interglacial stage, showing the ancient land areas (dotted) and the ancient river channels. The white crosses indicate Eolithic regions. From H. F. Osborn, *Men of the Old Stone Age*, after Averbury's *Prehistoric Times*, by permission of Charles Scribner's Sons.

depends upon the careful study of the movements of the great glaciers which covered the northern half of that continent during the four glacial stages (Table 44:2). The limits to which the ice cap extended in the last three glacial stages are shown in the maps (Fig. 44:8). The extent to which the ice cap extended in the first glacial stage was considerably less than that to which it extended during the second stage. The geography of western Europe during the Pleistocene was very different from what it is now (Fig. 44:9). The British Isles were connected with Europe and Iceland by a great land mass and what is now the Mediterranean Sea was largely dry land connecting Europe with Africa. The Thames flowed into the Rhine and the Rhine and the Elbe joined to form a river which flowed out into the Arctic Ocean. The Somme and the Seine were tributaries of a river which flowed through the English Channel into the Atlantic Ocean.

B. FOSSIL MEN

The rarity of primate fossils was mentioned at the beginning of this chapter and the conditions under which they lived given as a reason for this. The same is true of early human fossils. Not until man adopted the practice of burying his dead do human fossils become at all abundant. A further difficulty is presented by the uncertainty which often attends the exact dating of the remains. The methods used to determine geological chronology have already been discussed (Chap. 40). While it is usually possible to determine with certainty to which epoch a given Cenozoic stratum belongs it is much more difficult to determine where in the series of glacial and interglacial ages of the Pleistocene a given stratum belongs. A third uncertainty is introduced by the possibility that a fossil may have been moved from the site of its original formation into another stratum, by the action of water, ice, or even a human agency.

The fact that a fossil shows primitive characters does not necessarily mean that it belongs to an early stratum. The rate of evolution of organisms varies in different parts of the world and in different groups. Man is no exception. It is therefore to be expected that in early times men of different stages of culture and physical development existed simultaneously in different regions as they do on the earth at the present time. While in general the more primitive fossils are found in the earlier ages, exceptions occur. There is also some confusion with regard to the nomenclature applied to fossil men depending on whether certain types should be given the rank of separate genera or species.

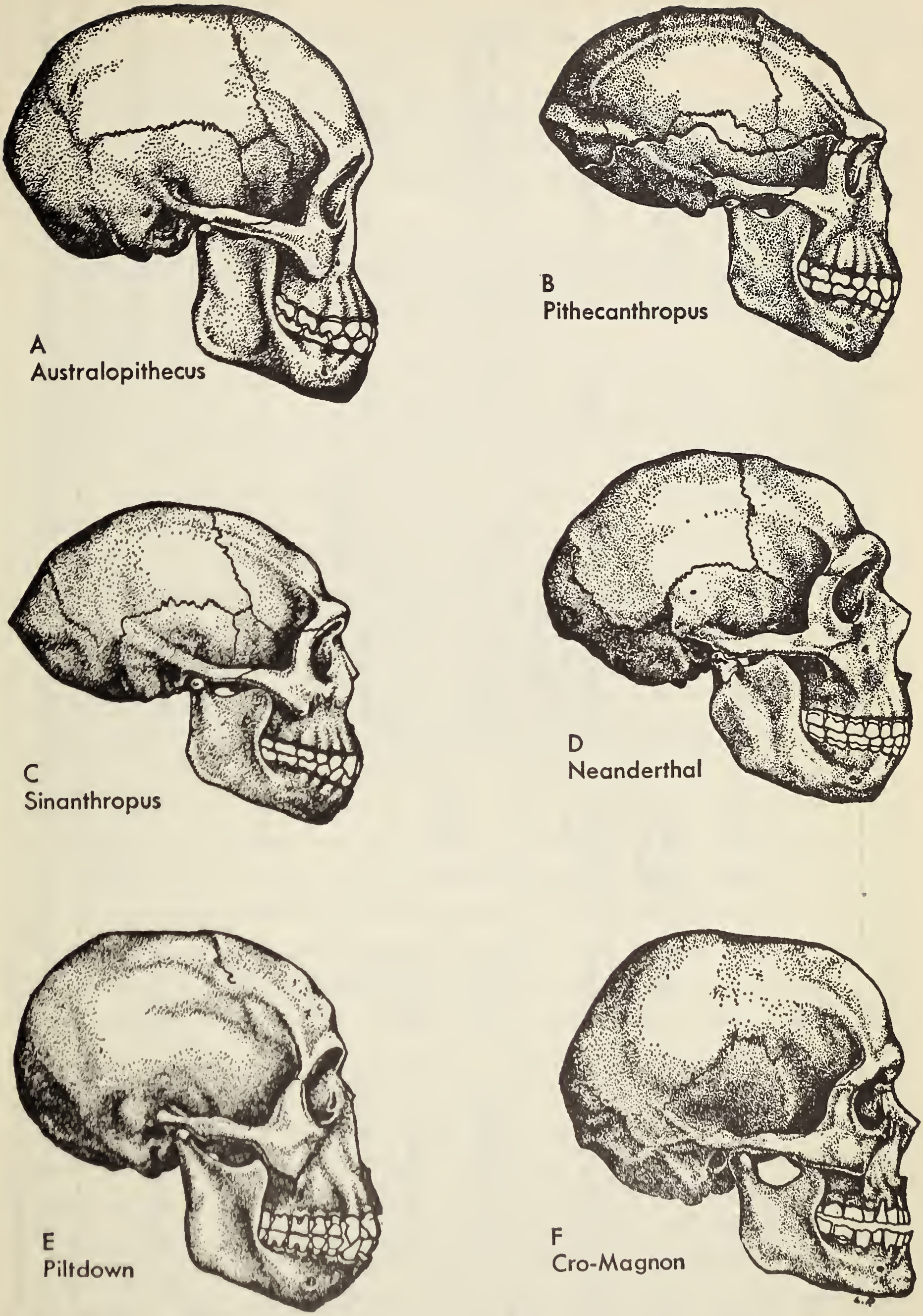


Fig. 44:10 A comparative series of skulls. A, after Dart and Brown; B, D, F, after McGregor; C, after Weidenreich; E, after Elliot Smith. From Romer, *Man and the Vertebrates*, University of Chicago Press.

TABLE 44:2. THE AGES OF MAN[1]

EPOCH	GLACIAL AGE	MEAN DATE YEARS B.C.	CULTURE AGE		FOSSIL MEN		DISTRIBUTION
					GENUS	SPECIES	
Recent	4th Interglacial		Age of Metals	Iron Age Bronze Age			
		25,000	Neolithic Mesolithic				World wide
Pleistocene Late	4th Glacial	150,000	Paleolithic Late	Magdelenian Solutrian Aurignacian	*Homo*	*sapiens*	Europe, Asia, Africa
	3rd Interglacial	175,000	Middle	Mousterian	*Homo*	*neanderthalensis*	Central, southern, and western Europe, Palestine
Middle	3rd Glacial	225,000					
	2nd Interglacial	550,000	Early	Acheulean	*Sinanthropus* *Pithecanthropus*	*pekingensis* *erectus*	North China Java
	2nd Glacial	630,000					
Early	1st Interglacial	950,000					
	1st Glacial	1,500,000		Chellean			
Pliocene			Eolithic				

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[1] Based on Schuchert and Dunbar, *Historical Geology*, p. 479, John Wiley & Sons, Inc., New York, and modified to conform with F. Weidenreich, in *American Anthropologist*, Vol. 42, N.S., 1940, p. 375.

These considerations should not be allowed to obscure the fact that there is fast becoming accumulated a large mass of well-established, definite, and precise evidence not only for the evolution of man but also for the course of that evolution.

Although the presence of worked flints in the Pliocene seems to show that man in some form existed in this epoch, the earliest human fossils come from deposits which are regarded as belonging to the Middle Pleistocene.

(1) FOSSIL MEN OF THE EARLY AND MIDDLE PLEISTOCENE, ASSOCIATED WITH EARLY PALEOLITHIC CULTURE: *PITHECANTHROPUS* AND *SINANTHROPUS*

Two types of primitive, early fossil men are known from the Middle Pleistocene, the Java ape-man, *Pithecanthropus erectus* (Gr. *pith*, ape + *anthropos*, man) and the Peking man, *Sinanthropus pekingensis* (Gr. *Sin*, China + *anthropos*, man). The first fossils of ***Pithecanthropus*** were found about fifty years ago, 1892, on the bank of a river in central Java near the town of Trinil and consist of a skull cap, a left femur, and three teeth found at one location and a lower jaw found in similar deposits 25 miles away. The beds in which the fossils were found are assigned to the Middle Pleistocene. More recent excavations on the bank of the same river but farther upstream near the town of Sangiran have yielded three more skull caps, one very well preserved, a lower jaw and an upper jaw; at Modjokerta in western Java the skull of a baby which is believed to belong to the same type has been found. Thus *Pithecanthropus erectus* is represented by five skulls, a few long bones, and a number of teeth. The fossils of ***Sinanthropus*** all come from an ancient cave at the village of Choukoutien about 30 miles from Peking (Peiping) in North China and were unearthed during the period between World Wars I and II. The deposits in which they were found are assigned also to the Middle Pleistocene. About fifty individuals, male and female, adult and juvenile, are represented. Of none of them is there an entire skeleton, a number being represented by teeth only. Strangely the remains consist chiefly of skull fragments, limb bones occurring only as fragments of seven thigh bones and one arm bone. There is no evidence of burial. They may have been left there by a group of head hunters. The fact that in most cases the base of the skull is broken, giving access to the cranial cavity, suggests cannibalism. The skulls may have been opened to extract the brain which may have been regarded as a delicacy just as the sheep's brain is now regarded. About four of the skulls are sufficiently well preserved to form a basis for reconstructions.

The fossils of *Pithecanthropus* and *Sinanthropus* show many similarities (Fig. 44:10). Indeed they are so similar that they undoubtedly ought to be placed in the same genus and perhaps in the same species. The original names are retained for convenience since they have become established in the literature. The cranium is low and its greatest breadth is in the region between the ears. Heavy, projecting supraorbital ridges protect the orbit. The posterior or occipital region is broad and rounded (Fig. 44:11). The foramen magnum is more posterior than in more recent skulls, indicating that the head projected forward. The lower jaw shows that there was no chin. The teeth although human in character resemble those of the manlike apes and there is a wide space, or diastema, between the canine tooth and the first molar. The average cranial capacity of the skull of *Pithecanthropus* is about 900 cubic centimeters while that of the *Sinanthropus* skulls is about 1000 cubic centimeters. While little is known of the rest of the skeleton what is known seems to point to a strong heavy-set body of medium height and an upright posture.

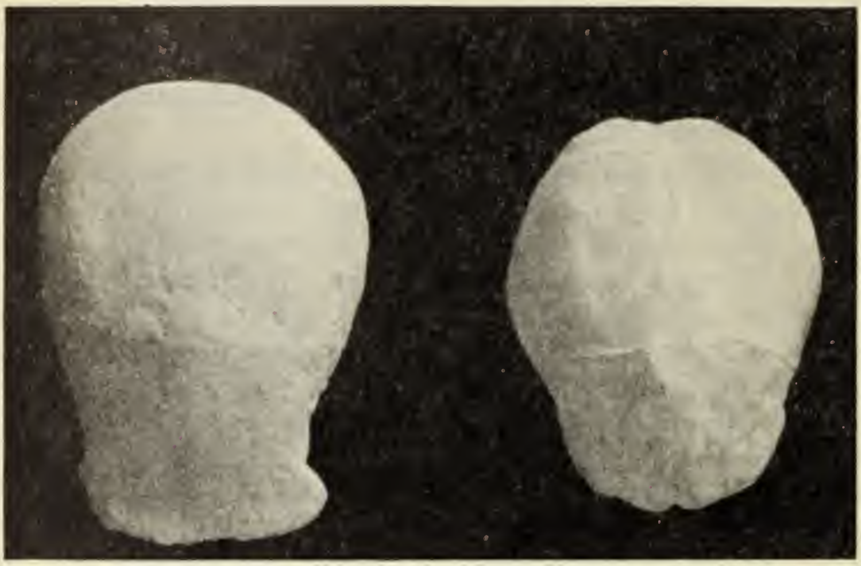

Fig. 44:11 *Pithecanthropus erectus*. Left, a view of the top of the cranium; at right, a cast of the inside of the top of the cranium, showing approximately the contour of the cerebral hemispheres. The front of the skull and brain are toward the lower part of the illustration. Photographs of casts in the American Museum of Natural History. Reproduced by permission.

Crude stone implements in the form of axes and scrapers attest to the employment of tools while black ashes and burned bones indicate the use of fire and the cooking of food. Casts of the cranial cavity of *Sinan-*

thropus indicate a marked development of that region of the brain which in modern man has been shown to lodge the motor center for speech, which would seem to indicate that he was capable of this method of communication.

A discussion of the human fossils from the Early and Middle Pleistocene would be incomplete without mention of a remarkable skull found at **Piltdown** in the south of England in a stratum which the geological evidence seems to show definitely belonged to the Early Pleistocene (First Interglacial). The fossils have been made the basis for the description of special human type to which the name ***Eoanthropus dawsoni*** (Gr. *Eo*, dawn) has been given. The remains consist of cranial fragments and most of a lower jaw. There seems some doubt whether all of the fragments belong to the same individual and as the cranial fragments do not fit together there has been much discussion of attempts to reconstruct the skull. However, certain features seem clear. The skull is very different from that of *Pithecanthropus* or *Sinanthropus*, the cranium is high, the supraorbital ridges are not prominent, the cranial capacity is considerably larger. According to one investigator the fragments of the cranium "cannot be distinguished from those of modern man, either in their general form or in individual features." The Piltdown skull therefore presents an enigma: either the geological or anatomical findings are not correct or there existed in England during the early Pleistocene a type of man very similar to the present inhabitants (Fig. 44:10).

(2) FOSSIL MEN OF THE MIDDLE AND LATE PLEISTOCENE ASSOCIATED WITH MIDDLE PALEOLITHIC (MOUSTERIAN) CULTURE: *HOMO NEANDERTHALENSIS*

All of the types of fossil men from the Late Pleistocene to the most recent, i.e., from the second interglacial on, have been placed in the genus *Homo*, the genus to which all the modern races of men belong. Nearly all of those which are limited to the Late Pleistocene are placed in the species *neanderthalensis*, named from the Neanderthal, a valley, near Dusseldorf, Germany, where one of the first skeletons of this type was found in 1858, associated with implements of the Mousterian culture. Since this discovery fifty or more skeletons, some remarkably complete and well preserved, have been unearthed in different parts of Europe, Asia, and Africa so that *Homo neanderthalensis* is known to have existed in Belgium, Germany, France, Spain, Italy, Croatia, Crimea, Palestine, Syria, Arabia, Iraq, and Rhodesia.

A comparison of the skeletons of Neanderthal men, women, and children with the skeletons of modern men, women, and children shows that the former were of lower stature, the adults being rarely over 5 feet 4 inches and probably averaging less than 5 feet, but of heavier build so that the average weight may have been equal to or greater than that of the average man or woman of today (Fig. 44:12). Had this species of man survived to our time he would probably have been a dangerous antagonist for any of our wrestling champions. He walked and stood in a slouch, his head forward and knees bent. His low forehead, massive ridges over large, round eyes, broad nose, and large hands and feet must have given him an appearance different from that of a man of any living race (Figs. 44:13, 44:14). The cranial capacity of the skull of Neanderthal man compares favorably with that of modern man, 1400–1600 cubic centimeters, but the shape of the brain as indicated by endocranial casts was somewhat different, the occipital portion being relatively larger, and the frontal portion relatively smaller than in modern man.

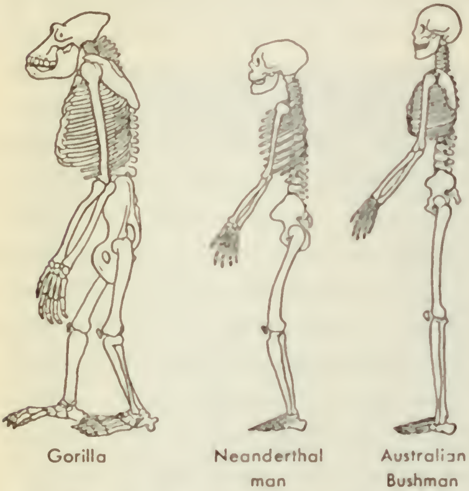

Fig. 44:12 Comparison of Gorilla, Neanderthal man and Australian Bushman. The scapula has been omitted from the Neanderthal skeleton. After Boule, *Fossil Men* by permission of Oliver and Boyd.

Recently there has been discovered in central Java near the town of Mgandong, in a deposit which is assigned to the third interglacial, the remains of a type of man which seems to have been intermediate between *Sinanthropus pekingensis* and *Homo neanderthalensis.* The type has been named ***Homo soloensis***, from the Solo River in the valley of which it was found. The fossil material comprises eleven skulls and skull fragments and two tibias. The cranial capacity averages about 1200 cubic centimeters. The greatest breadth of the brain was situated somewhat higher than in *Sinanthropus.*

(3) FOSSIL MEN OF THE LATE PLEISTOCENE AND RECENT, ASSOCIATED WITH LATE PALEOLITHIC AND SUBSEQUENT CULTURES: *HOMO SAPIENS*

Neanderthal man was succeeded by ***Homo sapiens*** (L. *sapiens*, wise), the species which includes all the races of modern man. The race which characterizes the Late Paleolithic is called **Cro-Magnon,** the name of a cave in the Dordogne in France where five skeletons were found. The

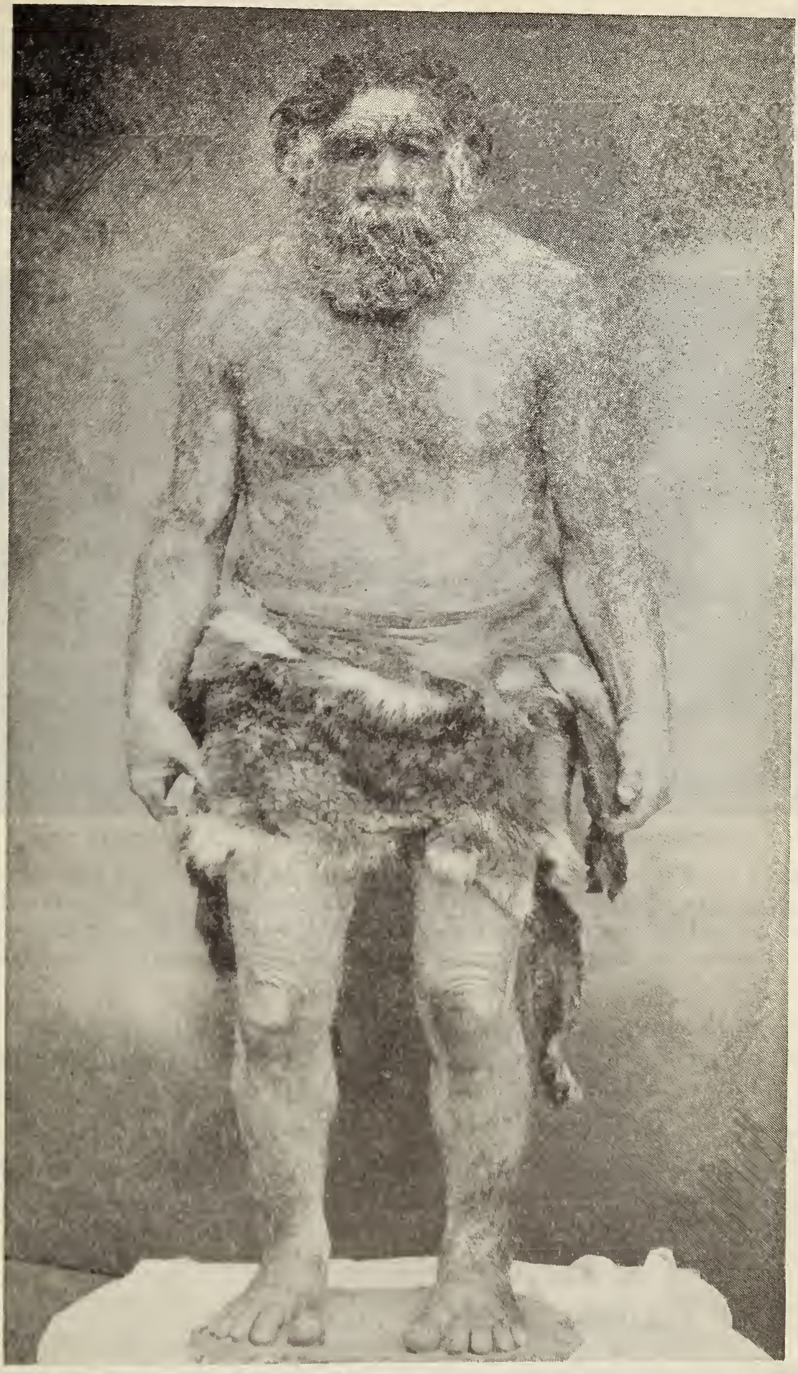

Fig. 44:13 Restoration of Neanderthal man. From a group by Frederick Blaschke. Photograph supplied by the Field Museum of Natural History and reproduced by permission.

Cro-Magnons were a handsome race of people and would compare favorably with any of the existing races of men. The skeletons, of which many have been found, indicate a height of 6 feet and an athletic build with strong muscles. The skulls (Figs. 44:10, 44:14) are remarkably large and dolichocephalic, i.e., the anterior-posterior diameter is large relative to the lateral diameter. The face was broad with large eyes far apart, large cheek bones, and wide jaws. The cranial capacity and therefore the size of the brain must have been equal to, if not greater than, that of the average European of today. There were probably other races of *Homo sapiens* in existence at the same time as the Cro-Magnons but they are imperfectly known and need not concern us here.

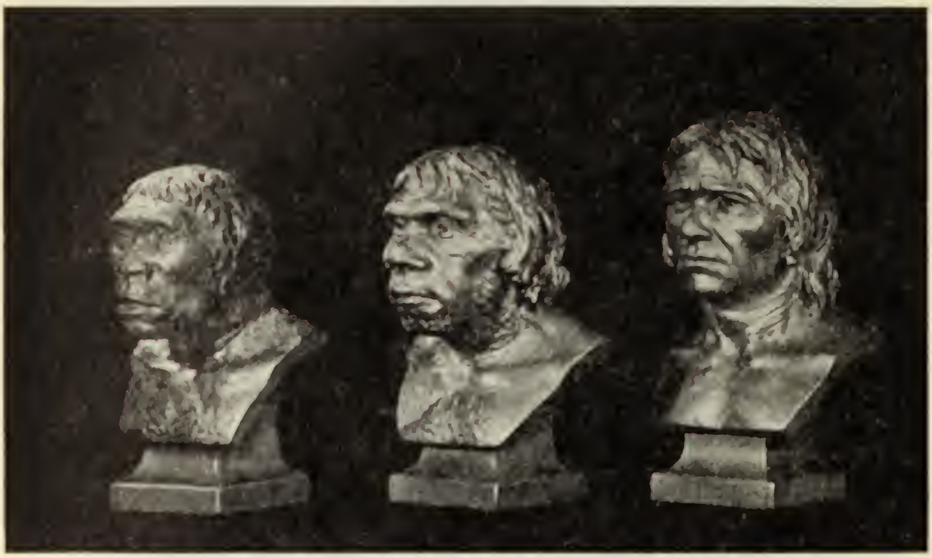

Fig. 44:14 Left to right, *Pithecanthropus erectus* or Java man, *Homo neanderthalensis* or Neanderthal man, and *Homo sapiens* represented by Cro-Magnon man. Restorations based on the skulls and the attachments of the facial muscles by J. H. McGregor. Reproduced by permission from a photograph supplied by the American Museum of Natural History.

It will not be necessary to consider the fossil men from the Recent epoch since their skeletons do not differ from those of the existing races of men.

C. THE CULTURAL AGES OF MAN

Man is distinguished from the anthropoid apes not only by his anatomical structure but also and more conspicuously by his use of tools and his social organization. So far as is known his first tools were of stone. It is fortunate for the prehistorian that early man used stone implements because such implements may be preserved almost indefinitely on or in the ground or in caves. Indeed stone implements provide the only record of the earliest men and even later when skeletal remains are available stone implements are more numerous and better preserved. This has led archeologists and prehistorians to use the stone implements to distinguish a series of "cultures" and to classify early man by his culture rather than by his physical features. The word **culture** is generally used to include the sum total of all the activities and achievements of a people but in this connection it is chiefly based on the types of stone implements. On this basis four main stages or "ages" are recognized in the evolution of mankind and are named, beginning with the earliest, Eolithic, Paleolithic, Neolithic, and the Age of Metals, the last being the age in which we now live. Within each age different cultures can be differentiated.

The Eolithic or Dawn Stone Age probably lasted through most of the Pliocene epoch and is by some believed to have extended back into the Miocene, which implies that it lasted for a million or more years and ended over a million years ago according to the chronology adopted in the table (Table 44:2). The Paleolithic or Old Stone Age corresponded in its duration to the Pleistocene epoch and lasted for about a million years. The Neolithic and the Age of Metals both occurred within the recent epoch. Compared with the Eolithic and Paleolithic, the Neolithic and the Age of Metals are but brief periods in man's long sojourn on earth. The relative duration of the Ages has varied in different parts of the world and in certain remote regions the Neolithic may be said to persist to the present time. The data given in Table 44:2 applies more particularly to western Europe.

(1) THE EOLITHIC OR DAWN STONE AGE CULTURE

As already stated the Eolithic probably corresponded in duration to the greater part of the Pliocene epoch. No human skeleton remains can with certainty be assigned to Pliocene deposits. The evidence for the existence of man in the Pliocene consists of certain rude stone implements called **eoliths** (Fig. 44:15) discovered in various parts of the Old World, chiefly in England, France, Germany, Egypt, and India. The best evidence is supplied by numerous chipped flints of various shapes and sizes found in the east and south of England in beds undoubtedly of the Pliocene epoch. The discussion hinges on whether these are the work of a human hand or merely the accidental effect of the rubbing and hitting of the stones in the bed of a stream or elsewhere. The opinion of experts is that most of the eoliths are the work of hands. We know little of the mode of life of Eolithic man beyond the character of the country in which he lived and the animals with which his existence was associated.

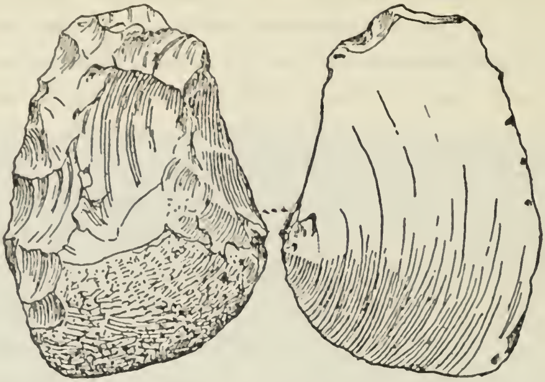

Fig. 44:15 Both sides of an eolithic flint scraper (natural size) from below Red Crag at Bramford, Ipswich. From Moir, *Antiquity of Man in East Anglia*, Cambridge University Press.

During the later part of the Pliocene, the time to which the eoliths belong, England had a warm, moist, temperate climate and was a land with forests and meadows where grazed elephants, horses, and cattle.

(2) THE PALEOLITHIC OR OLD STONE AGE CULTURE

The Paleolithic or Old Stone Age of man corresponds approximately to the Pleistocene epoch and lasted according to the chronology adopted in this text for about a million years. The men of the Old Stone Age have left a long and interesting record scattered in time and space over many parts of the Old World. Starting with the crudest implements and the skeletons of apelike men it ends in cultures very different from our own but showing a high degree of artistic and technical development and a physical type which must be recognized as the equal if not the superior of any modern man. In tracing the evolution of man during the Paleolithic it will be convenient to consider those of the Early, Middle, and Late Paleolithic in separate sections.

(a) THE CULTURE OF THE MEN OF THE EARLY PALEOLITHIC

The record left by Early Paleolithic man begins with certain rude stone implements and fragments of a few skeletons. The oldest and crudest of the stone implements are called **Chellean,** since they were first discovered at Chelles on the bank of the Seine near Paris (Fig. 44:16). In the case of the Chellean implements there is no doubt as to their being fashioned by a hand. The flints are worked into definite shapes and were used in a particular way. Some are recognized as hand axes, others as scrapers and borers which were probably used in preparing hides and in making tools from bone. The chipping of Chellean flints is crude and the edges jagged and irregular. Chellean implements have been found in Europe, Asia, and Africa.

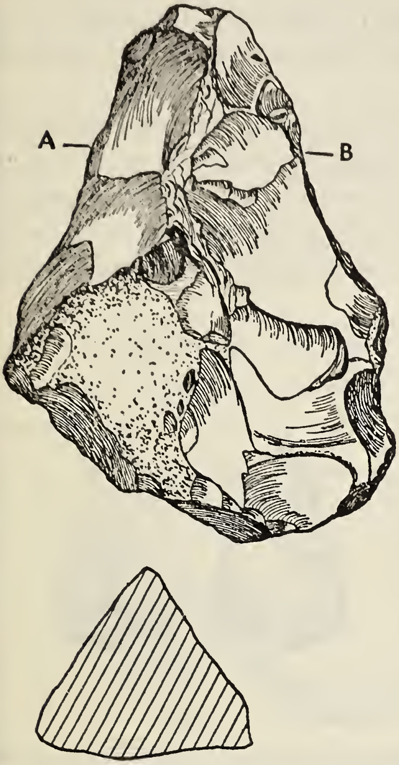

Fig. 44:16 Early Chellean hand axe from the Cromer Forest Bed in England. Below a section through the line AB. From Moir, *Antiquity of Man in East Anglia*, Cambridge University Press.

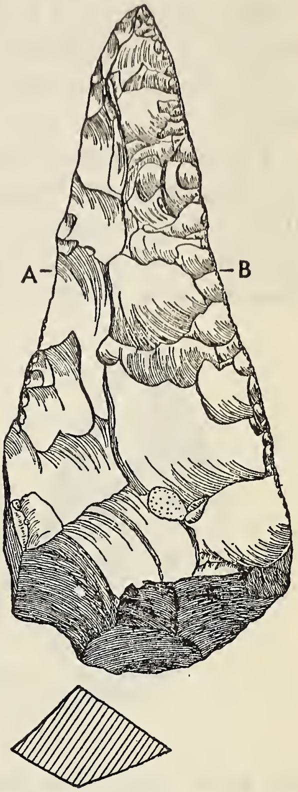

Fig. 44:17 Large Acheulean hand axe from Suffolk, England. Below a section through the line AB. From Moir, *Antiquity of Man in East Anglia*, Cambridge University Press.

More recent but still included in the Early Paleolithic is the Acheulean culture represented by stone implements which, although crude as compared to those of later times, were more skillfully made than those of the Chellean people. The chipping was more delicate and regular, leading to a keener and evener edge. The implements were more specialized as shown by a greater variety of forms (Fig. 44:17). Chellean and Acheulean flints are often of large size compared with those of later cultures.

(b) THE CULTURE OF THE MEN OF THE MIDDLE PALEOLITHIC

The record left by the men of the Middle Paleolithic, found in deposits of the latter part of the third interglacial and the beginning of the fourth glacial stages, is more detailed in regard to culture and skeletal remains than that of any previous stage. The term **Mousterian** has been applied to the culture of this time from Le Moustier, the name of the locality in the Dordogne in France where the culture was first carefully studied.

The men of this culture seem to have been of the type represented by the Neanderthal skeletons. They are frequently described as cave men. It is probable, however, that the greater part of their lives was spent in the open, and that in any case they lived at the entrances to caves rather than in them. At the entrances to these caves and in the near-by shelters formed by overhanging rocks are found the ancient hearths where they made their fires for cooking and for warmth. These men were great hunters and the bones found in and around the hearths show that they hunted the mammoth, rhinoceros, wild horse, bison, wild cattle, giant deer, and in later times the reindeer. The larger bones were split open, for the marrow was a delicacy then as it is today. The hides were undoubtedly used for various purposes and the bones were made into implements. Exactly how the men of Mousterian times captured and killed big game is somewhat of a mystery as their stone implements, which have been unearthed in great numbers, are not of large size.

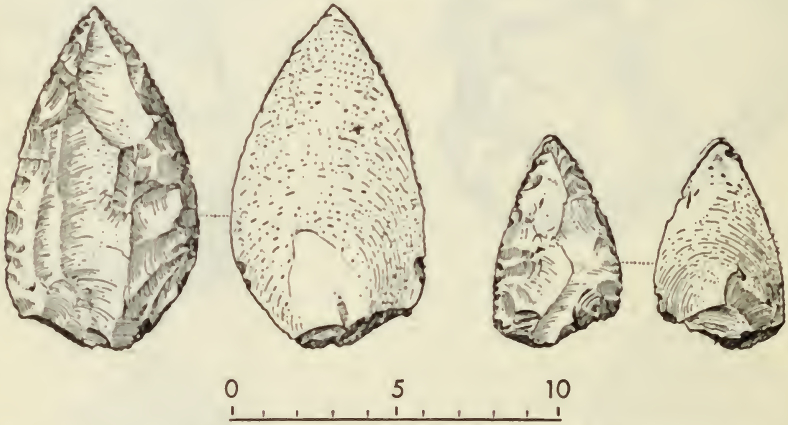

Fig. 44:18 Two typical Mousterian flint implements from Le Moustier. Each is made from a large flake of flint struck off from a nodule. One side, that shown on the left in each case, is chipped to make a sharp edge, while the other side is left with the original smooth surface of the flake. The scale below is in centimeters. After Déchelette, from H. F. Osborn, *Men of the Old Stone Age*, by permission of Charles Scribner's Sons.

Flints suitable for the making of implements are not found everywhere and Mousterian flints show that man was beginning to economize in the use of his raw materials. Chellean and Acheulean implements were made from entire nodules by chipping off flakes; Mousterian man made some of his implements from flakes skillfully chipped from large nodules and finished by finer chipping (Fig. 44:18). Some twenty or more different types of Mousterian implements with different uses have been found.

In Mousterian times man began to bury his dead. The deceased was carefully laid in a sleeping position and with him were buried flint implements and food. It is worth while to pause and think what this implies. First, belief in a life hereafter. Second, the expression of that belief in a burial ceremony. In other words, these early men were beginning to look outside themselves and to think beyond the material necessities of bare existence.

(c) THE CULTURE OF THE MEN OF THE LATE PALEOLITHIC

The Late Paleolithic lasted in the Old World for a much shorter time than either the Early or the Middle Paleolithic, occurring during the fourth glacial and extending into the beginning of the Recent epoch. Like their predecessors of Mousterian times, the men of the Late Paleolithic lived at the entrances to caves or in rock shelters. They subsisted mainly by hunting and fishing. Because the reindeer played an important role in their life, supplying food, clothing, and bone which they used extensively in their crafts, they have been called the **Men of the Reindeer Age**. In the Late Paleolithic a number of succeeding and progressive cultures are recognized, of which the most important are the Aurignacian, Solutrean, and Magdalenian, named after localities where extensive studies have been made.

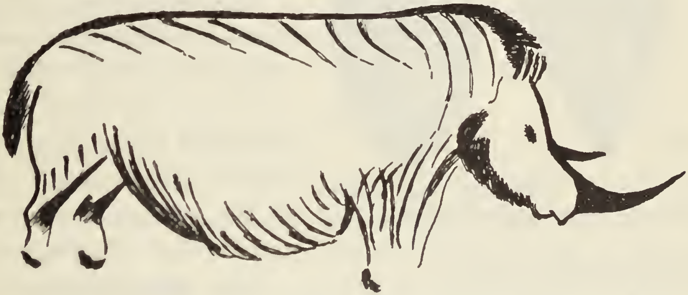

Fig. 44:19 Art of the Aurignacian period. The woolly rhinoceros, painted in red ochre with shading and partial representation of the hair, in the cavern of Font-de-Gaume, Dordogne, France. Redrawn after Breuil, from H. F. Osborn, *Men of the Old Stone Age*, by permission of Charles Scribner's Sons.

The **Aurignacian** culture which succeeded the Mousterian was characterized by the development of a number of different kinds of bone implements and the birth of art in the decoration of small personal belongings, ornaments and implements of stone, bone, and ivory, and in drawings, engravings, paintings, and bas-reliefs on the walls of caverns and grottos (Fig. 44:19). On account of their artistic ability, Aurignacians have been hailed the Greeks of the Paleolithic. Their art objects, like most primitive art objects, were undoubtedly used in the practice of magic and the observance of religious ceremonies.

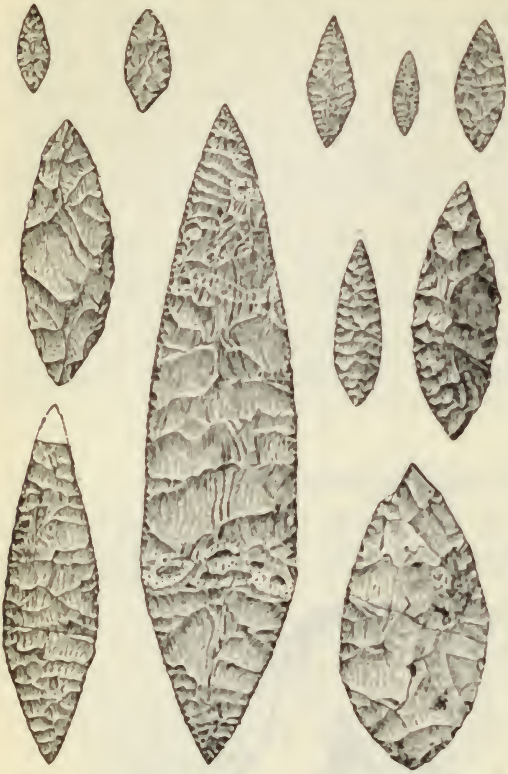

Fig. 44:20 Typical Solutrean flint implements of war and chase. After Mortellet, from H. F. Osborn, *Men of the Old Stone Age*, by permission of Charles Scribner's Sons.

The **Solutrean** culture is remarkable for the culmination of flint working. Never before or since has man made such beautiful spear heads and flint knives (Fig. 44:20). The art of the Aurignacians resembled that of the Solutreans.

The **Magdalenian** culture marks the end of the Old Stone Age. Bone tended to supplant flint in the construction of tools and many new kinds of bone implements, ornaments, and ceremonial objects appear, and sculpture in bone and ivory, especially of animal forms, was perfected.

(3) THE MESOLITHIC OR MIDDLE STONE AGE CULTURE

The **Mesolithic** culture was one of transition from the Late Paleolithic to the Neolithic. Small flakes of flint were much in use and bone replaced flint for some purposes and new uses were made of it. The culture was widespread in Europe, Asia, and Africa.

(4) THE NEOLITHIC OR NEW STONE AGE CULTURE

For information about the culture of the Neolithic peoples we are almost entirely dependent, as in the case of the cultures of the Paleolithic peoples, on tools, weapons, and other worked objects which have resisted the processes of decay, buried in the ground, hidden in caves or under water. The Neolithic is often termed the "Age of Polished Stone Implements," because the people of this age were the first to use grinding and polishing as a method of shaping and sharpening stone and flint (Fig. 44:21). However, Neolithic culture differs in many other and more important ways from that of the Paleolithic.

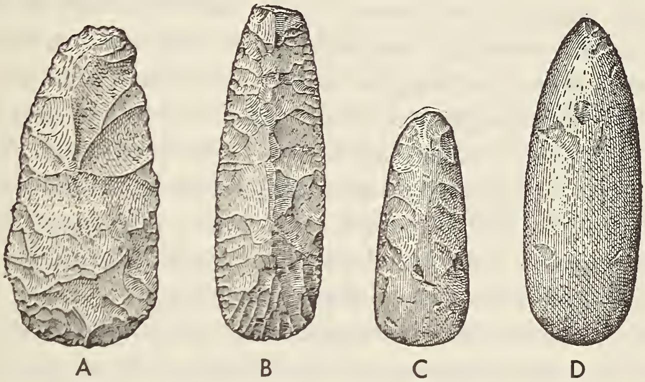

Fig. 44:21 Stages in the manufacture of the Neolithic Stone Axe. A, rough axe; B, axe chipped ready for polishing; C, axe partly polished; D, axe completely polished. After Mortellet, from H. F. Osborn, *Men of the Old Stone Age*, by permission of Charles Scribner's Sons.

The Neolithic Age began and ended early in Egypt, Mesopotamia, and Persia, occurred at a later date in western Europe, and persisted on the American continent up to the time of its discovery and settlement by white men.

First among the achievements of the Neolithic peoples must be placed agriculture and the domestication of animals. When and where these arts arose cannot be stated with certainty. Agriculture may have been discovered in the valley of the Nile in prehistoric Egypt for we know that barley and other cereals were cultivated there in very early times. From there it may have been introduced into Mesopotamia and Persia and later to the rest of the world. The barley and other cereals cultivated in Egypt were the native wild species. Wheat and barley were introduced into western Europe from the Mediterranean region. In Egypt the domestication of animals came after the discovery of agriculture. The first animal to be domesticated was the dog, but on prehistoric stone reliefs cows, asses, horned sheep, and goats are shown. Geese and ducks are also known to have been domesticated.

While the men of the Paleolithic lived in small, more or less isolated groups the people of the Neolithic tended to collect in larger groups, forming tribes. Some of these tribes were composed of pastoral peoples with herds of sheep, goats, and cattle. These people moved with their herds over the grasslands and lived in temporary shelters. Constantly on the move, such people must carry their few possessions and can practice only those industries requiring simple equipment. Such groups remain relatively small in numbers and develop only a simple social organization. Other tribes became farmers, cultivating grains and fruit trees. These people adopted permanent abodes and built huts or mud houses according to the materials available. The need for protection caused them to build their dwellings in villages or towns. The occupations of peoples living in villages and towns tend to become specialized and private property accumulates and comes to be recognized. All this leads to an increasing complexity of social organization. Thus the practice of agriculture may be said to be the chief cause of civilization (the word "civilization" comes from the Latin root, *civilis*, meaning a citizen or one capable of enjoying the privileges of a city).

Neolithic culture is also characterized by the invention of pottery for the storage of water and grain and for cooking. On account of its durability pottery, either as entire vessels or as broken fragments, is often found with the stone implements of this age. Among certain groups baskets took the place of clay pots for storage purposes. The textile arts were well developed in certain localities in the Neolithic. These include spinning, netting, knitting, weaving, and embroidery. Beautifully woven fabrics have been found preserved in the remains of Neolithic cultures in Switzerland and the United States.

One of the most important Neolithic inventions was seagoing boats, which were preceded by rafts and dugouts. These seagoing boats traversed the Mediterranean and skirted the west coast of Europe. During the Neolithic many wanderings and migrations of people occurred and it was probably during this age that the ancestors of the future Eskimos, Red Skins, Aztecs, and Incas came to the American continent from northeastern Asia by way of the Aleutian Islands and Alaska and wandered over the whole length and breadth of North and South America.

The problem of man's antiquity on the American continent is now engaging the interest of archaeologists. Recent finds of flint spear points with the remains of extinct animals near the small town of Folsom in New Mexico have made it seem probable that man was present in the Southwest and probably elsewhere on the American continent at least eight to ten thousand years ago or perhaps twice as long ago. The "Folsom points," as they are called, are equal in the quality of their workmanship to the finest flints of the Paleolithic in Europe. This would seem to indicate that the men who made them had reached a fairly advanced stage of culture. The American Indian as the white man found him when he discovered the continent is generally regarded as being in a Neolithic stage of culture comparable to the Neolithic of Europe.

(5) THE AGE OF METALS

Strange as it may seem, metals were long used for jewelry and to bring luck to the wearer before they were used in the manufacture of tools and weapons replacing stone. Doubt exists as to where metals were first discovered; some prehistorians favor Egypt, some Asia Minor, and some Persia. The first metal to be discovered seems to have been gold. This was followed by copper. Copper was probably discovered through the accidental heating of copper ore in a fireplace. Copper as found in Egypt is hard and suitable for making cutting instruments. It was soon found that tin added in small quantities to copper produced an alloy, called **bronze,** which is much harder than pure copper. The discovery spread far and wide and gave rise to the **Bronze Age.** The great poems of the Greek poet, Homer, the *Iliad* and the *Odyssey*, describe life in the Late Bronze Age. The shield of the hero Achilles was of bronze inlaid with silver and gold. Iron was a rare metal to the ancients and in the beginning was used for jewelry. A necklace found in a prehistoric grave in Egypt had iron beads alternating with gold. The Iron Age of archaeologists, however, does not begin until iron began to replace bronze for tools and weapons. The Iron Age seems to have begun about the same time in Egypt and Mesopotamia, namely between 1300 and 1200 B.C. For a considerable period both bronze and stone implements continued to be used with those of iron.

It is beyond the scope of this text to carry the story further into recorded history and the Machine Age in which we live.

4. SOME GENERAL REMARKS ON THE EVOLUTION OF MAN

Certain general features of the evolution of man become obvious from the data presented in this chapter. Most conspicuous is the extreme slowness with which man's physical form has evolved. Yet the rate of this evolution is not particularly slow when compared with other mammals, for example, the horse. If the term man is restricted to the genus *Homo*, it may be said that man began his existence about half a million years ago. In the beginning there may have been a number of different species; gradually, as the result either of extinction or amalgamation, these species became reduced in number until only one remained.

Until quite recently man's cultural and social evolution has been also extremely slow, perhaps slower than the evolution of his body. Homo sapiens existed for many thousand years before he discovered agriculture. Since then his cultural and social development has been exceedingly rapid, so rapid that as yet there has been no noticeable change in the structure of his body including the brain in the period since the beginning of civilization, which is probably not more than ten thousand years in Egypt and perhaps half that in western Europe. The evolution of social life and its development into various types of civilization, which must be regarded as the most outstanding characteristic of modern man, appears therefore to be not primarily a matter of the evolution of the individual and the formation of new species as outlined in the previous chapter (Chap. 43), The Mechanism of Organic Evolution. The forces which produce and the principles which govern the evolution of societies and the origins of new civilizations would therefore appear to be different from those which are involved in the evolution of individual organisms and the origin of new species.

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Questions

1. Compare the structure of one of the higher apes with that of man.
2. Outline briefly four theories of the origin of man from primate stock.
3. Name the ages of man and state approximately the duration of each.
4. What is known about Early Paleolithic man?
5. Compare Neanderthal man with modern man and with the great apes.
6. Give reasons for our knowing more about Neanderthal man than about any of his human predecessors.
7. When does *Homo sapiens* appear in the geological record?
8. Name the culture periods included in the Late Paleolithic. How are they distinguished?
9. How did the culture of the Neolithic peoples differ from that of all previous cultures?
10. Discuss briefly the Age of Metals and compare it with the Neolithic.

Suggestions for Further Reading

Schmucker, Samuel Christian, *Man's Life on Earth*, The Chautauqua Press, Chautauqua, New York, 1925.

Hooton, Earnest A., *Up from the Ape*, The Macmillan Company, New York, 1937.

Romer, Alfred Sherwood, *Man and the Vertebrates*, The University of Chicago Press, Chicago, 1933.

Osborne, Henry F., *Men of the Old Stone Age*, Charles Scribner's Sons, New York, 3rd ed., 1918.

APPENDIX

A Synoptic Table of the Plant and Animal Kingdoms

While it is desirable and logical to define the groups, phylum, class, order, and family in exact terms and in such a way as to make it possible to assign any organism to its phylum, class, order, and family by an inspection of a few outstanding characteristics, actually this presents many difficulties, and is not the method which systematists pursue in practice. The fundamental concept seems to be that of the genus; this concept of a genus as expressed frequently in the popular name of an animal or plant seems to antedate systematic biology. A family is primarily a group of similar genera. Similarly an order is a group of similar families and so on. The groups thus become more and more abstract as one goes up the scale and more difficult to define in precise concrete terms, or in easily recognized characters. This is particularly true in such groups as the flowering plants and birds where there are numerous genera and evolution seems to be taking many different directions.

APPENDIX A

The Plant Kingdom and Its Subdivisions[1]

PHYLUM THALLOPHYTA (Thal-loph′y-ta, Gr. *thallus*, a young shoot + *phyton*, a plant). The body of these plants consists of a thallus. A thallus is without true roots, stem, or leaves. It may consist of a single cell or an aggregate of cells showing little differentiation into tissues. Sex organs, when present, are typically one celled. Spore-bearing organs single celled.

Subphylum Algae (Al′gae, L. *alga*, a seaweed). Thallophytes possessing chlorophyll and manufacturing their own food materials.

CLASS CYANOPHYCEAE (Cy′an-o-phy′ce-ae, Gr. *cyanos*, a dark blue substance + *phycos*, a seaweed). Commonly called **blue-green algae** since a blue pigment is associated with the chlorophyll. A red pigment is sometimes present in addition to the blue so that the plants appear reddish. The Red Sea owes its color to one of these organisms. The Cyanophyceae are regarded as the simplest of the Algae and perhaps are the most primitive of existing plants. There is no distinct nucleus although there is a central colorless body which seems to take its place. The plant body consists of single cells or cells adhering to form filaments. Examples: *Gleocapsa*, *Aphanocapsa*, *Nostoc*, *Anabaena Oscillatoria* (Fig. 8:1).

CLASS CHLOROPHYCEAE (Chlo′ro-phy′ce-ae, Gr. *chloros*, light green + *phycos*, a seaweed). Commonly called **green algae** because of their color. The chlorophyll is associated with another green pigment. The plant body is single celled, filamentous, or platelike. The cells have definite nuclei and the chlorophyll is contained in chloroplasts. Most of the Chlorophyceae occur in either fresh or salt water but some are found on the surface of the soil and one form, *Protococcus*, is responsible for the green patches often seen on the bark of trees. Included in this class are the microscopic plants called **diatoms** which are common in fresh water and play an important role in the life of the open ocean. Examples: *Protococcus*, *Volvox* (Fig. 18:8), *Spirogyra*, *Ulva*, diatoms, desmids (Fig. 8:6), *Chara*, *Nitella*.

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[1] The technical terms used in describing the different groups are defined in the text where they may be found by consulting the index. In the examples generic names begin with a capital, common names with a small letter. In some cases the common names include more than the members of a single genus, e.g., diatoms, desmids; in other cases, especially among the flowering plants and trees, the common name may indicate a particular species.

CLASS PHAEOPHYCEAE (Phae′o-phy′ce-ae, Gr. *phaios*, dusky + *phycos*, a seaweed). Commonly called **brown algae**. The chlorophyll is associated with a brown pigment. Multicellular, often large algae, exclusively marine, and usually found between tide marks where they are the commonest seaweeds, the class includes the largest and most highly differentiated of the algae. Some, like kelp, are said to reach a length of 300 feet, thus rivaling the largest trees. Examples: rockweed (*Fucus*) (Fig. 8:7), Sargassum weed (*Sargassum*), kelp (*Laminaria*, *Nereocystis*) (Fig. 3:3).

CLASS RHODOPHYCEAE (Rho′do-phy′ce-ae, Gr. *rodon*, rose + *phycos*, a seaweed). Commonly called **red algae**. The chlorophyll is associated with a red pigment. Multicellular, mostly marine, and generally found below low tide. In some species the body consists of fine, delicate branches of great beauty. One group in which the cell walls become impregnated with calcium carbonate plays a part in the building of coral reefs. Example: *Polysiphonia*.

Subphylum Fungi (Fun′gi, L. *fungus*, a mushroom). Thallophytes which lack chlorophyll and except in the case of certain bacteria live as saprophytes or parasites.

CLASS SCHIZOMYCETES (Schiz′o-my-ce′tes, Gr. *schizein*, to split + *myces*, *mycetos*, fungus). Sometimes called **fission fungi**, more frequently, **bacteria**. Unicellular. Without a visible nucleus and without pigment. Bacteria occur everywhere where there are living things. Many are beneficial in causing the decay of organic materials and making new life possible, others are able to take nitrogen from the air and by making it available for other plants are thus important in agriculture, still others are the cause of plant and animal diseases. The bacteria are considered in Chap. 9. Example: bacteria (Fig. 9:1).

CLASS MYXOMYCETES (Myx′o-my-ce′tes, Gr. *myxos*, slime + *myces*, *mycetos*, fungus). Plant body a protoplasmic mass or plasmodium containing numerous nuclei but not divided into cells. Found on decaying leaves and rotting wood where they form slimy masses. Sometimes claimed by zoologists as animals on account of their locomotion by pseudopodia and their ability to take in solid food particles. Their reproduction is plantlike and they form spores with cellulose walls. Example: slime mold.

CLASS PHYCOMYCETES (Phy′co-my-ce′tes, Gr. *phycos*, a seaweed + *myces*, *mycetos*, fungus). Commonly called **algal fungi** because of their resemblance to certain *Algae*, especially in the form of their plant body which consists of fine filaments or hyphae and in their method of reproduction. The hyphae are multinucleate and not divided into cells. Some species, for example the bread mold, cause decay while others, like the downy mildews, cause plant diseases. Examples: bread mold (*Rhizopus*) (Fig. 8:9), downy mildews.

CLASS ASCOMYCETES (As′co-my-ce′tes, Gr. *askus*, a sac + *myces*, *mycetos*, fungus). Commonly called **sac fungi.** The plant body consists of branching hyphae which have cross walls (septa). Spores are produced in asci. This is the largest class of the Fungi containing many saprophytic or parasitic species. In the curious plants called **lichens** which really consist of two plants, an alga and a fungus living together, the fungus partner is a member of this class. Examples: yeast (*Saccharomyces*) (Fig. 8:14), cup fungi (*Peziza*) (Fig. 8:11), powdery mildew of lilac (*Microsphaera*).

CLASS BASIDIOMYCETES (Ba-sid′i-o-my-ce′tes, L. *basidium* (see below) + *myces*, *mycetos*, fungus). Commonly called **basidium-forming fungi.** A basidium is a special cell with slender branches (usually four) on the ends of which the spores are produced. The class includes the smut fungi which are all parasites and occur chiefly on grasses and the common cereals. They destroy annually many millions of dollars' worth of corn, oats, barley, wheat, and rye. Also in this class are the rust fungi, parasitic forms which attack seed plants including the cereals and are of equal if not greater economic importance than smut fungi. Lastly come the fleshy and woody fungi better known as mushrooms, puffballs, and shelf fungi. Examples: smut fungi, rust fungi (Fig. 8:15), mushrooms (Figs. 3:4, 8:16), puffballs (Fig. 39:7), bracket fungi.

PHYLUM BRYOPHYTA (Bry-oph′y-ta, Gr. *bryon*, moss + *phyton*, plant). The division includes the liverworts and mosses. Small plants usually found in moist regions. The life cycle shows a marked alternation of sexual and asexual generations. The conspicuous plant is the sexual or gametophyte generation and produces gametes. The zygote is parasitic on the gametophyte and develops into an asexual sporophyte producing spores.

CLASS HEPATICAE (He-pat′i-cae, L. *hepar*, *hepatis*, liver). So named because of the shape of the lobes of the gametophyte which in the simpler forms is a flattened thallus. These plants occur in moist shady places, some on the ground, some on rocks usually about waterfalls or springs, and some actually float on the surface of the water in marshes. The creeping habit of the simpler **liverworts** suggests the way in which land plants arose from algae along the margins of marshes. In the more highly developed forms the body of the gametophyte is differentiated into stem and leaves (leafy liverworts). Example: liverworts (Figs. 10:1–10:4).

CLASS MUSCI (Mus′ci, L. *muscus*, a moss). The gametophyte has an erect stem and spirally arranged leaves. The **mosses** are the most familiar and most numerous of the bryophytes. Also the plant bodies of both the gametophyte and sporophyte generations reach their highest development in this class of the division. They form carpets on the floors of forests and are often an important part of the vegetation of rocky lands and barren wastes. Example: mosses (Figs. 3:5, 10:6–10:12).

PHYLUM PTERIDOPHYTA (Pter′i-doph′y-ta, Gr. *pteris*, *pteridos*, a fern + *phyton*, a plant). There is an alternation of sexual and asexual generations as in the Bryophyta. The conspicuous plant is the sporophyte which is independent and has leaves, stem, and roots. The gametophyte is a small, short-lived, independent plant. The sperms are motile and water is required for fertilization (Figs. 11:1–11:15).

CLASS FILICINEAE (Fil′i-cin′e-ae, L. *filix*, *filicis*, fern). Commonly called **ferns.** The familiar fern plant consists of an underground stem which bears numerous leaves or fronds. Spores are formed on the under sides of the fronds. They develop into small gametophyte plants consisting of a thallus bearing sex organs. The zygotes develop into young fern plants (sporophytes) which are at first dependent on the gametophytes. Ferns are by far the commonest group of the Pteridophytes. They reach their greatest development in the tropics where they may attain the proportions of trees. Such tree ferns were abundant in the Carboniferous period and contributed to the formation of the coal beds. Examples: *Pteris* (brachen fern), *Marsilia*, *Salvinia*, and *Azolla* (last three genera are water ferns) (Figs. 3:6, 11:1).

CLASS EQUISETINEAE (Eq′ui-se-tin′e-ae, L. *equus*, horse + *seta*, bristle). Commonly called **horsetails.** These plants are usually found in sandy soil along railway tracks or the margins of ponds. They are the humble survivors of a group of once numerous and large plants which helped to form the great forests of the coal age. The conspicuous part of the plant consists of straight upright jointed stems which in some species resemble little bamboo plants and in others take on a bushy shape with numerous branches. Scalelike leaves circle the stem at the joints. The upright stems arise from creeping underground stems. At the tips of some of the upright stems cones are formed consisting of spore-bearing leaves. The spores develop into small gametophyte plants which consist of a thallus bearing sex organs. Example: horsetail (*Equisetum*) (Fig. 11:11).

CLASS LYCOPODINEAE (Ly′co-po-din′e-ae, Gr. *lycos*, wolf + *pous*, *podos*, foot). Commonly called **club mosses** or **ground pines,** or **lycopods.** Certain species are common in our northern forests. The familiar plant consists of a creeping stem, often buried under the dead leaves of the forest floor, which gives off upright stems which bear cones. The leaves are small like those of a moss and arranged spirally. The cones consist of spore-bearing leaves. The gametophytes to which the spores give rise are small, rare, inconspicuous plants. Examples: *Lycopodium* (ground pine) (Fig. 11:12), *Selaginella* (club moss) (Fig. 11:13).

PHYLUM SPERMATOPHYTA (Sper′ma-toph′y-ta, Gr. *sperma*, *spermatos*, seed + *phyton*, a plant). Commonly called **seed plants.** This division contains all the common herbs, bushes, and trees which make up the bulk of the vegetation of the earth. It includes all of the flowering plants and the cone-bearing trees and shrubs. The cone of a pine tree, although very different in appearance from the flower of a lily, is essentially similar. Both bear spores on modified leaves. Two kinds of spores are formed. One kind, the pollen, is borne on the stamens of the flower and on the staminate scales of the small staminate cones of the pine and gives rise to minute male plants. The other kind is borne on the carpels of the flower and on the carpellate scales of the larger carpellate cones of the pine and gives rise to minute female plants. The male plant developed from the pollen must reach the female plant to bring about fertilization. This is usually accomplished by some outside agent, such as wind or insects, carrying the pollen from one plant to the carpels or carpellate scales of another. The eggs in the female plants are then fertilized and develop into embryos. Development is then arrested and the embryo is enclosed in protective coverings to form a seed. The development of seeds is a method of reproducing and scattering the species and is an adaptation to life on land.

CLASS GYMNOSPERMAE (Gym′no-sper′mae, Gr. *gymnos*, naked + *sperma*, a seed). This subdivision includes most of our large evergreen trees and shrubs. Cones take the place of flowers and the seeds which are formed on the carpellate cones are not enclosed in an ovary as in the flowering plants.

ORDER CYCADALES (Cyc′a-da′les, from *cycas*, a cycad). The large divided leaves are borne on the top of a short, thick, unbranched stem giving to the plant a palmlike appearance. The seeds are borne on cones. Motile sperms are formed by the male gametophyte plants after the pollen has reached the carpellate cone scales on which the female gametophytes develop. Tropical and semitropical. Examples: cycads (genera *Cycas* and *Zamia*).

ORDER GINKGOALES (Gink′go-a′les, Japanese *ginkgo*, the ginkgo tree). Represented by the peculiar and interesting ginkgo tree (genus *Ginkgo*). Example: Maidenhair tree (Ginkgo).

ORDER CONIFERALES (Co′ni-fer-a′les, L. *conus*, a cone + *ferre*, to bear). Commonly called **conifers**. This order, which contains most of the gymnosperms, includes nearly all of the common evergreen trees and shrubs. Great forests of coniferous trees make up, especially in the north temperate lands, a large portion of the vegetation of the earth. The cones are of two kinds, staminate, which produce pollen, and carpellate, which bear spores producing female gametophytes and eventually seeds. Examples: pine (*Pinus*) (Fig. 13:1), spruce (*Picea*), fir (*Abies*), larch (*Larix*), juniper (*Juniperus*), Douglas fir (*Pseudotsuga*), redwood (*Sequoia*), hemlock (*Tsuga*).

ORDER GNETALES (Gne-ta′les, from *gnetum*, the gnetum tree). Climbing or erect shrubs or small trees. The single genus is interesting because its method of reproduction shows many resemblances to the next subdivision, the Angiosperms. Tropical or semitropical. Example: Gnetum.

CLASS ANGIOSPERMAE (An′gi-o-sper′mae, Gr. *aggeion*, vessel or receptacle + *sperma*, a seed). The name refers to the seeds being enclosed in an ovary. Commonly called **flowering plants.**[1]

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[1] Botanists have found that in arranging and classifying flowering plants the family is the most useful group. However for the purposes of showing the extent of variation and the evolution of the Angiosperms the orders are more important. For this reason the orders are emphasized in the following classification, the more common families being listed. The student who wishes to determine the names and families of flowers is advised to use a key, preferably one adapted to his own locality or, failing that, Gray's *Handbook of Flowering Plants*. See references at the end of Chap. 3.

Subclass Dicotyledoneae (Di-cot′y-le-do′ne-ae, Gr. *dis*, twice + cotyledon, the name given to a seed leaf). Name refers to there being two seed leaves. Leaves generally net veined. Parts of flower (sepals, petals, stamens, carpels) usually in fives, fours, or twos.

ORDER RANALES (Ra-na′les), the buttercup order. This order is a large one and is by many regarded as being nearest to the primitive stem from which all flowering plants arose. It includes both woody and herbaceous plants. The typical flower, well represented by the buttercup, has separate sepals, petals, stamens, and carpels (i.e., is complete) although petals are sometimes lacking and the carpels may be united. The carpels are numerous and arranged on a more or less cone-shaped axis (receptacle). The order includes the Ranunculaceae or buttercup family, the Anonaceae or papaw family, the Lauraceae or laurel family, Magnoliaceae or magnolia family, the Berberidaceae or Barberry family, and the Nymphaeceae or water-lily family.

ORDER MALVALES (Mal-va′les, L. *malva*, mallow). The mallow order. A common order including herbs, shrubs, and trees. Typically the flower resembles that of a buttercup, being regular and hypogynous with separate sepals and petals and numerous stamens and pistils. The order includes the Malvaceae or mallow family, the Ulmaceae or elm family, and the Urticaceae or nettle family.

ORDER GERANIALES (Ge-ra′ni-a′les, from geranium). The geranium order. Herbs or shrubs. Flowers resembling those of the Malvales but with fewer stamens and carpels, being regular and hypogynous. Sepals five, petals five, stamens five to ten, carpels five united. The order includes the Geraniaceae or geranium family.

ORDER PAPAVERALES (Pa-pav′er-a′les, L. *papaver*, poppy). The poppy order. Usually herbs. Petals and sepals usually four, carpels two or more, ovary superior. The order includes the Cruciferae or mustard family, and Papaveraceae or poppy family.

ORDER CARYOPHYLLALES (Car′y-o-phyl-la′les, Gr. *caryo*, nut + *phyllon*, leaf). The pink or carnation order. Flowers typically with stamens and pistil (i.e., perfect) and sepals and petals (i.e., complete). Usually four to five sepals, four to five petals, stamens twice as many as sepals, single pistil composed of one to five carpels. Petals may be absent. The order includes the Caryophyllaceae or pink family, the Polygonaceae or buckwheat family, and the Salicaceae or willow family.

ORDER PRIMULALES (Prim′u-la′les, from primrose). The primrose order. Mostly herbs. Flowers with stamens and pistil (i.e., perfect), sepals and petals (i.e., complete), regular and pentamerous. Single superior pistil. Stamens adnate to petals. The order includes the Primulaceae or primrose family, and the Plantaginaceae or plantain family.

ORDER ERICALES (Er′i-ca′les, L. *erice*, heath). The heather order. Usually shrubs, often with leathery leaves. Flowers regular, perfect, pentamerous, sympetalous. Ovary superior. The order includes the Ericaceae or heather family.

ORDER GENTIANALES (Gen′ti-a-na′les, from *Gentiana*, the gentian genus). The gentian order. Flowers regular, perfect, usually pentamerous, ovary superior and formed of two carpels. Petals are lacking in the Oleaceae. The order includes the Gentianaceae or gentian family, and the Oleaceae or olive family.

ORDER POLEMONIALES (Pol′e-mo′ni-a′les, from *Polemonium*, the genus of the Greek valerian). The phlox order. Mostly herbs or climbers. Flowers typically regular but irregular in some families, pentamerous, sympetalous. Stamens adnate to petals, same number as lobes of corolla and alternate with them. Ovary superior, formed of two or three carpels. The order includes the Polemoniaceae or phlox family, the Convolvulaceae or morning-glory family, and the Boraginaceae or forget-me-not family.

ORDER SCROPHULARIALES (Scroph′u-la′ri-a′les, from the genus *Scrophularia*). The snapdragon order. Flowers typically irregular. Stamens less (two or four) than the lobes of the sympetalous corolla. Ovary superior, formed of one or two carpels. The order includes the Scrophulariaceae or snapdragon family.

ORDER LAMIALES (La′mi-a′les, from *Lamium*, the mint genus). The mint order. Mostly herbs. Flowers irregular, often two-lipped. Stamens two or four. Ovary superior, two celled, often deeply four lobed. The order includes the Labiatae or mint family.

ORDER ROSALES (Ro-sa′les, L. *rosa*, a rose). The rose order. Flowers resemble those of the Ranales and are typically perfect, regular to irregular, polypetalous. Perianth pentamerous. Stamens indefinite in number and free, carpels few to many, separate or united. A large order with many families. The order includes the Rosaceae or rose family and the Leguminosae or bean family.

ORDER MYRTALES (Myr-ta′les, from the name of the myrtle genus, *Myrtus*). Woody or herbaceous plants. Flowers regular and perfect, ovary inferior, stamens usually numerous. The order includes the Myrtaceae or myrtle family and the Onagraceae or evening-primrose family.

ORDER CACTALES (Cac-ta′les, L. *cacti*, a kind of prickly plant). Plants of arid regions with fleshy or woody stems, often leafless and green. Flowers perfect, usually regular with numerous sepals and petals. Ovary inferior. The order includes the Cactaceae or cactus family.

ORDER CELASTRALES (Cel′as-tra′les, from the genus *Celastrus*). The bittersweet order. Mostly trees, shrubs, or woody climbers. Flowers regular. The order includes the Celastraceae or bittersweet family, and the Vitaceae or grape family.

ORDER SAPINDALES (Sap′in-da′les, from *Sapindus*, the soapberry). The maple order. Usually trees or shrubs. Flowers numerous and small, perfect, usually regular. The order includes the Aceraceae or maple family, the

Juglandaceae or walnut family, the Fagaceae or oak family, and the Betulaceae or birch family.

ORDER UMBELLALES (Um′bel-la′les, from *umbel*, a type of inflorescence). The parsley order. Woody or herbaceous plants. Flowers arranged in umbels, small, perfect, regular, typically tetramerous or pentamerous. Ovary inferior. The leaves are often compound and more or less finely divided. The order includes the Cornaceae or dogwood family, and the Umbelliferae or parsley family.

ORDER RUBIALES (Ru′bi-a′les, L. *rubia*, madder). The madder order. Woody trees, shrubs, or herbs with opposite, usually simple leaves. Flowers usually in a cymose inflorescence, tetramerous or pentamerous, sympetalous. Stamens adnate to petals. Ovary inferior. The order includes the Rubiaceae or madder family.

ORDER CAMPANULALES (Cam-pan′u-la′les, L. *campanula*, a little bell). The bluebell order. Mostly herbs, some woody. Flowers in a racemose inflorescence, perfect, sympetalous. Ovary inferior. Anthers often form a tube. The order includes the Campanulaceae or bluebell family.

ORDER ASTERALES (As′ter-a′les, L. *aster*, a star). The aster order. The largest order of flowering plants. Mostly annual or perennial herbs but a few are shrubs or low trees. Many small flowers on a common receptacle forming a head. Corolla tubular. Stamens adnate to corolla. Ovary inferior. The order includes the family Compositae often called composites.

Subclass Monocotyledoneae (Mon′o-cot′y-le-don′e-ae, Gr. *monos*, one + *cotyledon*, seed leaf). The name refers to there being one seed leaf. The leaves are generally parallel veined. Parts of flower usually in threes.

ORDER ALISMALES (Al′is-ma′les, Gr. *alisma*, water plantain). The water plantain order. Herbs found chiefly in marshes and ponds. Flowers without calyx or corolla or with a conspicuous perianth. Carpels one to many, separate, superior. The order includes the Alismaceae or water plantain family, the Typhaceae or cattail family, the Najadaceae or pondweed family, and the Pontederiaceae or pickerelweed family.

ORDER LILIALES (Lil′i-a′les, L. *lilium*, a lily). The lily order. Generally herbs which are perennial by means of a bulb or underground stem, rarely shrubs or trees. Flowers usually regular and with the parts in threes. Ovary usually three celled. The order includes the Liliaceae or lily family.

ORDER ARALES (A-ra′les, L. *arum*, the arum "lily"). The arums and duckweeds. Mostly tropical herbs which often attain a considerable size. Leaves generally large, often branched. Flowers small and inconspicuous in an often huge inflorescence. The order includes the Araceae or arum family, and the Lemnaceae or duckweed family.

ORDER PALMALES (Pal-ma′les, L. *palma*, a palm). The palm order. Tropical trees. Stem unbranched with a crown of large leaves. Flowers small in a usually much-branched inflorescence enclosed in a huge spathe. The order includes the Palmaceae or palm family.

ORDER GRAMINALES (Gra′mi-na′les, L. *gramen*, *graminus*, grass). The grasses and sedges. Annual or perennial herbs. Stem slender, with elongated internodes and alternate, linear, parallel-veined leaves divided into sheath and blade. Flowers small, naked, or with a perianth represented by scales or hairlike structures. About eight hundred species. Economically they are the most valuable group of plants since they are the principal source of food for man and domestic animals. The order includes the Gramineae or grass family and the Cyperaceae or sedge family.

ORDER IRIDALES (I′ri-da′les, L. *iris*, a sweet-smelling plant). Flowers are regular and the ovary is inferior. The order includes the Amaryllidaceae or amaryllis family and the Iridaceae or iris family.

ORDER ORCHIDALES (Or′chi-da′les, Gr. *orchis*, a testicle). The orchid order. The name refers to the tubers of the genus, *Orchis*. Perennial herbs. The flowers are irregular and in many cases show intricate adaptation to insect pollination. Stamens reduced to one or two and united with pistil. The order includes the Orchidaceae or orchid family.

APPENDIX B

The Animal Kingdom and Its Subdivisions

PHYLUM PROTOZOA (Pro′to-zo′a, Gr. *protos*, first + *zoon*, animal). Small animals consisting of a single cell or colonies of single cells or of protoplasm which does not show a division into cells. Protozoa occur in fresh water, the sea, the soil, and as parasites in other animals. The phylum is divided into four classes largely on a basis of method of locomotion and protoplasmic structure.

CLASS SARCODINA (Sar′co-di′na, Gr. *sarx*, flesh + *eidos*, like). Slow-moving protozoa in which the locomotion is brought about by means of pseudopodia. The body shape is irregular and changing, the protoplasm being limited only by a delicate plasma membrane. One of the best known is *Amoeba* (Figs. 3:10, 18:1, 18:3). This genus occurs both in fresh water and in the sea. The Foraminifera (Fig. 18:6) are a large group of the Sarcodina which form minute, often snaillike shells. So abundant have these organisms been in certain geological periods that some calcareous rocks consist almost entirely of their shells. Another important group of this class are the Radiolaria. These animals form beautiful internal skeletons which in many cases are composed of silica. The floor of the deep parts of the great oceans is covered with their dead skeletons which form a radiolarian ooze. There are also parasitic Sarcodina, the best known genus being *Endamoeba* (Fig. 18:5). One species (*E. coli*) occurs as a harmless parasite in man while another (*E. histolytica*) causes the amoebic dysentery of the tropics.

CLASS MASTIGOPHORA (Mas-ti-goph′o-ra, Gr. *mastix*, whip + *phereiv*, to bear). Often called **flagellates.** Usually small, rapidly moving protozoa in which the chief method of locomotion is by means of **flagella.** The body usually retains a more or less definite shape due to a cuticle covering the plasma membrane. *Euglena* (Fig. 18:7) is a relatively large form which occurs in fresh water. Colonial forms in which a number of individuals are united are common. One of these is *Volvox* (Fig. 18:8) which occurs in fresh water as beautiful green spheres visible to the naked eye. Much of the phosphorescence which makes the path of a vessel at sea white at night is due to myriads of Dinoflagellates. Many animals harbor flagellate parasites. The best known genus is *Trypanosoma* (Fig. 18;9), one species of which, *T. gambiensis*, may pass part of its life cycle in the human blood and cause the frequently fatal disease known as African sleeping sickness.

CLASS INFUSORIA (In′fu-so′ri-a, E., infusion). Called also **ciliates.** Active protozoa moving by means of cilia and retaining a fairly fixed body form. Cilia are slender protoplasmic extensions which differ from flagella in being fairly rigid, moving in a fixed plane, and usually much more numerous on any particular animal. Like the Mastigophora the body of the Infusoria is covered by a cuticle or pellicle. There is usually a definite mouth through which food particles are taken into the body and a definite anus through which the undigested portions are extruded. Typically the nucleus consists of two parts, a macronucleus which controls the vegetative activities of the animal and a micronucleus which plays an important role in sexual reproduction. Infusoria are abundant in both fresh and salt water and occur frequently as parasites in other animals. One of the best known is *Paramecium* (Figs. 18:10, 18:11–18:12), the slipper animalcule of fresh-water ponds and hay infusions. Other common genera also occurring in fresh water are *Stentor*, *Stylonychia*, *Carchesiam*, and *Vorticella* (Fig. 18:15).

CLASS SPOROZOA (Spo-ro-zo′a, Gr. *sporos*, spore + *zoon*, animal). Parasitic Protozoa which live in the tissues of other animals which act as hosts. Except in certain stages of the life cycle they are incapable of locomotion. Reproduction is by means of spores. Often there is more than one host and the life cycle cannot be completed without the transfer of the parasite from host to host. One order, Gregarinida, is especially common as parasites of lower animals (invertebrates), particular insects; another, Coccidia, is parasitic mostly in higher animals (vertebrates); while a third, Haemosporidia, is parasitic in the blood of vertebrates. The latter includes the well-known malarial parasite, *Plasmodium* (Fig. 18:16), which causes malaria in man.

PHYLUM PORIFERA (Po-rif′e-ra, L. *porus*, pore + *ferre*, to bear). These animals, commonly called **sponges,** are irregular in shape and in the adult stage are usually attached to rocks or other objects in the water. There are a few fresh-water sponges but most species are marine. The outer surface of the body contains numerous fine pores (hence the scientific name) which communicate with canals leading into a gastral cavity which in turn leads to the outside by a larger opening known as the osculum. Water enters by the pores and after passing through the gastral cavity passes out by the osculum. The current of water is maintained by peculiar flagellated cells called collar cells on account of the collar surrounding the attached part of the flagellum. The skeleton consists of microscopic spicules interwoven to form the structure recognized as a sponge when the living matter is removed. There are many species of sponges. They differ chiefly in the form of the gastrula cavity and the composition and structure of the spicules. About a dozen different species are used for bath sponges (Figs. 3:11, 25:2).

PHYLUM COELENTERATA (Coe-len′te-ra′ta, Gr. *coilos*, hollow + *entera*, intestines). These animals are radially symmetrical and possess a central gastrovascular cavity or coelenteron opening to the exterior by a mouth usually surrounded by tentacles. The body consists of only two layers of cells, the ectoderm, or epidermis, and the endoderm, or gastrodermis, separated by a noncellular layer of jelly. Scattered especially in the ectoderm are stinging cells or nematocysts.

CLASS HYDROZOA (Hy′dro-zo′a, Gr. *hydra*, Hydra + *zoon*, animal). The individual polyps are small but often form colonies of considerable size. The body of the polyp is the simplest found in the phylum Coelenterata. There is no gullet and the mouth opens directly into a saclike coelenteron or gastrovascular cavity which is not divided. There is usually an alternation of generations. The polyps reproduce asexually by budding to form medusae or jellyfish. The medusae are bell-shaped and are distinguished from those of the Scyphozoa by the possession of a velum or membrane extending inward from the margin of the bell. The mouth is on the end of a manubrium which hangs down from the center of the bell like a clapper. The medusae reproduce sexually, the eggs and sperms arising from ectodermal cells. In the fresh-water hydra, which is commonly used as a laboratory type, there is no alternation of generations, the solitary polyps producing both eggs and sperms which unite to form a zygote which passes through a short larval stage (planula) to develop into a new polyp. Examples: *Hydra* (Fig. 2:7), *Obelia* (Fig. 19:2), *Goneonemus* (Fig. 19:3), *Physalia.*

CLASS SCYPHOZOA (Scy′pho-zo′a, Gr. *skyphos*, cup + *zoon*, animal). In this class the conspicuous stage is a medusa or jellyfish, sometimes of large size. The coelenteron is somewhat more complicated than that of the Hydrozoa and consists of a series of branched radial canals united by a circumferential canal. There is no velum. The medusa reproduces sexually, the eggs and sperm being formed from endodermal cells. The zygote may develop directly into a new medusa or there may be a relatively small and inconspicuous stage corresponding to the polyp of the Hydrozoa from which medusae are budded off. A common form is the large marine jellyfish, *Aurelia* (Figs. 19:5, 19:6).

CLASS ANTHOZOA (An′tho-zo′a, Gr. *anthos*, flower + *zoon*, animal). The individuals are often of fair size and occur either singly or combined to form colonies. All known species are marine. The mouth leads into a gullet lined with epidermis. The coelenteron is partitioned by endodermic membranes called mesenteries extending radially from the gullet to the body wall. The polyps reproduce sexually, eggs and sperm being formed from endodermal cells located in reproductive organs on the mesenteries. There is no alternation of generations. The zygote develops into a small ciliated organism (planula) which becomes attached to a rock or other aquatic object and develops into a new polyp. Examples: sea-anemones (Figs. 3:12, 19:7), corals (Fig. 19:8).

PHYLUM PLATYHELMINTHES (Plat′y-hel-min′thes, Gr. *platus*, flat + *helmins*, *helminthes*, worm). Commonly referred to as **flatworms.** The body is elongate and wormlike but not divided into segments. It is bilaterally symmetrical with anterior and posterior ends. In addition to ectodermal and endodermal layers there is a middle layer of mesoderm. The cells are differentiated into tissues forming organs. The animals occur in fresh and salt water, on land, and as parasites in other animals.

CLASS TURBELLARIA (Tur′bel-la′ri-a, L. *turbo*, a whirling [motion]). Commonly referred to as **planarians.** Free-living flatworms with flat oval bodies which move through the water with a graceful undulating motion which is produced by ciliated epidermal cells which cover the body. They are especially common among the vegetation of fresh-water ponds and the seashore. The mouth is on the ventral surface and there is often a muscular pharynx which can be extruded to capture prey. Examples: *Planaria*, *Dendrocoelum* (Figs. 3:13, 20:1).

CLASS TREMATODA (Trem′a-tod′a, Gr. *trematodes*, having holes [i.e., suckers]). Commonly called **flukes.** Parasitic. No cilia in adult stage. A digestive cavity but no anus. Suckers on ventral surface. Example: liver fluke of sheep (*Fasciola*) (Fig. 20:6).

CLASS CESTODA (Ces′tod-a, Gr. *cestos*, girdle + *eidos*, like). Commonly called **tapeworms.** Parasitic. No mouth or alimentary canal. The tapeworm (best considered as a colony) consists of a series of segments (individuals) called proglottids budded off from a head or scolex. Example: pork tapeworm (*Taenia*) (Figs. 20:8–20:10).

CLASS NEMERTINEA (Nem′er-ti′nea, Gr. *nemertes*, unerring). Often called **nemertian worms.** Mostly free living and marine. Alimentary canal with mouth and anus. There is a long proboscis separate from the alimentary canal which is retracted into a sheath from which it is extruded.

PHYLUM NEMATHELMINTHES (Nem′a-thel-min′thes, Gr. *nema*, thread + *helmins*, *helminthes*, worm). Commonly called **roundworms.** The body is bilaterally symmetrical and not segmented. The digestive tract is a long tube with mouth and anus. The animals occur in fresh and salt water, the soil, and as parasites in the bodies of other animals and plants. Examples: "vinegar eel," hookworm, roundworm of the horse (*Ascaris*), *Trichina* (Figs. 3:14, 21:1).

PHYLUM ROTIFERA (Ro-tif′e-ra, L. *rota*, wheel + *ferre*, to bear). Commonly called **rotifers** or **wheel animalcules** because of the arrangement of the cilia in two circular bands near the mouth. Microscopic, free-living, fresh-water, multicellular, unsegmented animals with jaws inside the pharynx and usually the hind end developed into a foot for temporary attachment (Figs. 3:15, 25:6).

PHYLUM BRYOZOA (Bry′o-zo′a, Gr. *bryon*, moss + *zoon*, animal). Commonly called **moss animals.** Found in colonies usually attached to plants, rocks, or the shell of other animals. The individual animals are minute, attached, aquatic forms, but they usually form colonies of plainly visible size. Alimentary canal U-shaped (Figs. 3:16, 25:7).

PHYLUM BRACHIOPODA (Brach′i-op′o-da, Gr. *brachion*, arm + *pous*, *podos*, foot). Commonly called **lamp shells** from the resemblance of their shells to the primitive type of lamp. Body covered by a vivalve shell, one valve ventral, the other dorsal (Fig. 25:8).

PHYLUM ECHINODERMATA (E-chi′no-der′ma-ta, Gr. *echinos*, sea urchin + *derma*, skin). The name refers to the spines which often cover the surface. The body is radially symmetrical, usually on a pattern of five, and is supported by a skeleton of plates. Locomotion is by means of tube feet. They occur only in the sea.

CLASS ASTEROIDEA (As′ter-oi′de-a, Gr. *aster*, star + *eidos*, like). Commonly called **starfishes.** Typically with five arms not sharply marked off from a central disc. Starfish (*Asterias*) (Fig. 39:40).

CLASS OPHIUROIDEA (O′phi-u-roi′de-a, Gr. *ophis*, snake + *oura*, tail + *eidos*, like). Commonly called **brittle stars.** Typically five arms sharply marked off from a central disc.

CLASS ECHINOIDEA (Ech′i-noi′de-a, Gr. *echinus*, sea urchin + *eidos*, like). Commonly called **sea urchins.** Without arms, spherical, heart shaped or disc shaped (Fig. 3:17).

CLASS HOLOTHURIOIDEA (Hol′o-thu′ri-oi′de-a, Gr. *holothurion*, holothurian + *eidos*, like). Commonly called **sea cucumbers.** Shaped like a cucumber. Skeletal plates small and separated making the body flexible.

CLASS CRINOIDEA (Cri-noi′de-a, Gr. *crinon*, lily + *eidos*, like). **Sea lilies.** Arms branched, central disc with stalk for attachment. Mostly deep-sea forms and fossils (Fig. 40:4).

PHYLUM MOLLUSCA (Mol-lus′ca, L. *molluscus*, soft bodied). Commonly called **mollusks.** Soft-bodied animals often covered with a protective shell of calcium carbonate. They move by means of a muscular organ, the foot. All excepting some snails and slugs live in water and most are marine.

CLASS AMPHINEURA (Am′phi-neu′ra, Gr. *amphi*, both + *neuron*, nerve). Commonly called **chitons.** Flattened bilateral mollusks in which the shell consists of eight transverse plates. Example: chiton (*Chiton*) (Fig. 39:39).

CLASS GASTROPODA (Gas-trop′o-da, Gr. *gaster*, stomach + *pous*, *podos*, foot). Commonly called **snails** or **slugs.** Usually a single coiled shell, sometimes (slugs) no shell. Examples: land snails (Fig. 3:18), nudibranches or sea slugs, boat shells, periwinkles, water snails, oyster drill (Fig. 39:38), periwinkles (Fig. 39:42), slugs (Fig. 39:9), conch (*Busycon*) (Fig. 39:54).

CLASS CEPHALOPODA (Ceph′a-lop′o-da, Gr. *kephale*, head + *pous*, *podos*, foot). Commonly called **cephalopods.** There is a well-developed head with large eyes surrounded by long prehensile tentacles. Exclusively marine. Examples: squid (Fig. 39:56), octopus, devilfish, nautilus, and fossil forms (Figs. 40:4, 40:5).

CLASS PELECYPODA (Pel′e-cyp′o-da, Gr. *pelekus*, hatchet + *pous*, *podos*, foot). Commonly called **bivalves.** Shell consists of two lateral "valves." Examples: oyster, scallop (Fig. 39:53), clam (Fig. 39:50), mussel (Fig. 39:37).

PHYLUM ANNELIDA (An-nel′i-da, L. *annulus*, ring). Commonly called **segmented worms.** The body, which is bilaterally symmetrical and wormlike in shape, is composed of a longitudinal series of transverse segments which appear as transverse rings on the exterior. They occur in fresh and salt water and in the soil.

CLASS CHAETOPODA (Chae-top′o-da, Gr. *chaite*, hair + *pous, podos*, foot). Annelids with either stiff hairlike projections (setae) or fleshy outgrowths of the body wall (parapodia) or both.

ORDER POLYCHAETA (Pol′y-chae′ta, Gr. *polus*, many + *chaite*, hair). Commonly called **polychaetes.** Mostly marine worms. With fleshy outgrowths called parapodia. Examples: clamworm (*Nereis*) (Fig. 39:52), *Amphitrite* (Fig. 3:19).

ORDER OLIGOCHAETA (Ol′i-go-chae′ta, Gr. *oligos*, few + *chaite*, hair). Commonly called **oligochaetes.** Mostly fresh water or terrestrial. Setae but no parapodia. No distinct head. Example: earthworm (*Lumbricus*) (Fig. 22:1).

CLASS HIRUDINEA (Hir′u-din′e-a, L. *hirudo*, leech). Commonly called **leeches.** No setae or parapodia. Body consists of 32 segments. Two suckers, one surrounding the mouth, the other at the tail end.

PHYLUM ARTHROPODA (Ar-throp′o-da, Gr. *arthron*, joint + *pous, podos*, foot). Commonly called **arthropods.** The body is enclosed in an outer hard chitinous covering or exoskeleton which is jointed to allow movement and is bilaterally symmetrical and segmented like that of annelids; the segments are more differentiated however, so that a head, thorax, and abdomen can usually be distinguished. Arthropods are the most numerous in species of all the phyla.

CLASS CRUSTACEA (Crus-ta′ce-a, L. *crusta*, hard outer surface). Arthropods which usually spend their entire life in water and breathe by means of gills. Examples: copepods, fish lice, barnacles (Fig. 39:36), crayfish (Fig. 39:32), *Hippa* (Fig. 39:48), crabs (Figs. 39:43, 39:51), lobsters (Fig. 39:55), shrimps, sow "bug" (Fig. 39:9).

CLASS TRILOBITA (Tri′lo-bi′ta, L. *tri*, three + *lobos*, lobe). Extinct marine arthropods which were very numerous in early geologic time (Fig. 40:4).

CLASS ONYCHOPHORA (On′y-choph′o-ra, Gr. *onus, onuchos*, claw + *pherein*, to bear). Peculiar wormlike arthropods which show a relationship to the Annelida. There are only a few species, all of which live on land in the tropics.

CLASS CHILOPODA (Chi-lop′o-da, Gr. *cheilos*, lip + *pous, podos*, foot). Commonly called **centipedes.** Body flattened. Segments, except those of the head and tail, similar and each bearing one pair of legs. In moist dark places living on vegetable matter (Fig. 3:20).

CLASS DIPLOPODA (Di-plop′o-da, Gr. *diploos*, double + *pous, podos*, foot). Commonly called **millipedes.** Body cylindrical, apparent segments except those of the head and tail similar and each bearing two pairs of legs. (Each apparent segment is really two segments.) In moist dark places living on vegetable matter.

CLASS INSECTA (In-sec′ta, L. *insectus*, divided [body]). Arthropods which breathe air by means of air tubes or tracheae. The body of the adult is usually divided into head, thorax, and abdomen. Head bears one pair of antennae. The thorax bears three pairs of legs and usually two pairs of wings. The more highly developed groups of insects pass through a metamorphosis or change of form in their life cycle, the young animal or larva, often called grub or worm, being quite different in its structure and mode of life from the adult. To effect the change from larva to adult the animal may go into a quiescent stage forming a pupa or cocoon. There are more species of insects than of all other animals put together. The characters most commonly used in classifying insects are type of metamorphosis, wings, and mouth parts. Some insects go through their life cycle without a metamorphosis (ametabolic), the larva being similar to the adult. Others have a gradual or partial metamorphosis (hemimetabolic), the young animals, known as *nymphs*, changing gradually into adults without any resting or pupal stage. Still others have a complete metamorphosis (holometabolic), the larva forming a pupa or cocoon in which it undergoes an extensive reorganization into the adult which is often very different from it not only in structure but in mode of life. Typically an insect has two pairs of wings. These, however, may be absent or there may be only a single pair. Further, both pairs may be membranous (dragonflies) or the front pair may be parchmentlike (grasshoppers), or form a protective covering (beetles), or both pairs may be covered with scales (butterflies and moths). The mouth parts may be adapted for chewing, piercing and sucking, sucking only, or vestigial (i.e., reduced to such an extent as to be useless) (Fig. 24:9).

ORDER THYSANURA (Thys′a-nu′ra, Gr. *thysanos*, tassel + *oura*, tail). Commonly called **bristletails.** Primitive wingless insects with larval stages resembling adults. Chewing mouth parts. Eleven abdominal segments. Usually two or three long, thin, caudal appendages. Found under bark, among dead leaves, etc., and in buildings. Examples: silverfish, firebrat.

ORDER COLLEMBOLA (Col-lem′bo-la, Gr. *colla*, glue + *embolon*, peg). Commonly called **springtails.** Very small, often microscopic, primitive, wingless insects with larval stage resembling adult. Chewing or sucking mouth parts, six abdominal segments. Springing organ on ventral side of fourth abdominal segment. Examples: snowfleas, garden fleas.

ORDER ORTHOPTERA (Or-thop′te-ra, Gr. *orthos*, straight + *pteron*, wing). Commonly called **grasshoppers, locusts,** etc. Metamorphosis is gradual, the larvae being known as nymphs. Usually two pairs of wings, the forewings hard and straight, the hind wings folding under. Chewing mouth parts. Most are vegetable feeders but some are carnivorous. Widely distributed. Examples: walking-stick insects, mantids, cockroaches, crickets, grasshoppers (Figs. 3:21, 23:13).

ORDER ISOPTERA (I-sop′te-ra, Gr. *isos*, equal + *pteron*, wing). Commonly called **termites** or **white ants.** Small social insects often mistaken for true ants. Metamorphosis gradual, larvae somewhat resembling parents, no pupal stage. Chewing mouth parts. Abdomen jointed directly to thorax.

Feed chiefly on dead wood. Found in tree stumps and near decaying wood. Examples: white "ants" or termites (Fig. 24:6).

ORDER NEUROPTERA (Neu-rop′te-ra, Gr. *neuron*, nerve + *pteron*, wing). Commonly called **dobson flies, ant lions,** etc. Larvae which are often aquatic go through a pupal stage (complete metamorphosis). Adults with four membranous wings which, when at rest, are held rooflike over the body. Chewing mouth parts in adults, often sucking mouth parts in larvae. Mostly carnivorous. Examples: dobson "flies," lacewinged "flies," aphis lions, ant lions, the larvae of the latter called **doodlebugs.**

ORDER EPHEMEROPTERA (E-phem′e-rop′te-ra, Gr. *ephemeros*, lasting but one day + *pteron*, wing). Commonly called **May flies.** Metamorphosis gradual. Nymphs aquatic. Adult with two pairs of membranous wings, the forewings larger. Mouth parts of larvae for chewing, those of adults reduced and useless since adult does not feed.

ORDER ODONATA (O-don′a-ta, Gr. *odous*, *odontos*, tooth). Commonly called **dragon flies** and **damsel flies.** Metamorphosis gradual. Nymphs aquatic. Adult with two pairs of membranous wings, hind wings larger. Chewing mouth parts. Feed chiefly on other insects. Dragon fly (Fig. 39:33).

ORDER PLECOPTERA (Ple-cop′te-ra, Gr. *plecos*, plaited + *pteron*, wing). Commonly called **stone flies.** Metamorphosis gradual. Nymphs aquatic, usually in running water under stones. Adults with two pairs of wings, the hind wings larger and folded in plaits when at rest. Larva with chewing mouth parts which are frequently reduced in adult which does not eat.

ORDER CORRODENTIA (Cor′ro-den′ti-a, L. *corrodens*, gnawing). Commonly called **book lice.** Metamorphosis gradual. Small insects. Adult wingless or with two pairs of wings. Chewing mouth parts. Feed on fungi, lichens, paste in books.

ORDER MALLOPHAGA (Mal-loph′a-ga, Gr. *mallos*, wool + *phagein*, eat). Commonly called **bird lice.** No metamorphosis. Chewing mouth parts. No wings. Eyes degenerate. Feed on feathers and scales of birds, some on hair of mammals.

ORDER THYSANOPTERA (Thy′sa-nop′te-ra, Gr. *thysanos*, fringe + *pteron*, wing). Commonly called **thrips.** Small insects with a gradual metamorphosis. Piercing mouth parts. Wingless or with two pairs of long, narrow, membranous wings. Most feed on plants, others on insect eggs and aphids. May be found in daisies or clover flowers. The onion thrip is a serious pest.

ORDER ANOPLURA (An′o-plu′ra, Gr. *an*, without + *oplon*, sting + *oura*, tail). Commonly called **sucking lice.** Small wingless insects parasitic on the skin and hair of mammals, without metamorphosis. Mouth parts piercing and sucking. All the members of this order are external parasites of mammals and feed on their blood. Examples: the head louse (*Pediculous humanus capitis*) (Fig. 24:8), the human crab louse (*Phthirius pubis*), the body louse or cootie (*Pediculus humanus corporis*), also many species on domesticated animals.

ORDER HEMIPTERA (He-mip′te-ra, Gr. *hemi*, half + *pteron*, wing). Commonly called **true bugs.** Metamorphosis gradual. Mouth parts piercing and sucking. Two pairs of wings, the front pair thickened at the base. Some with no wings. Most feed on plant juices, some on blood. Examples: water boatmen, back swimmers, water bugs, electric-light bugs, water striders, leaf bugs, bedbugs (*Cimex lectularius* (Fig. 24:8) is the human species), assassin bugs, lace bugs, chinch bugs, squash bugs, stink bugs.

ORDER HOMOPTERA (Ho-mop′te-ra, Gr. *homos*, same + *pteron*, wing). Commonly called **cicadas, leaf hoppers, aphids.** Metamorphosis gradual. Usually two pairs of similar wings which are held rooflike over the body when at rest. Mouth parts for piercing and sucking. Nearly all feed on plant juices. Examples: cicadas, spittle insects, tree hoppers, leaf hoppers, plant lice, phylloxerids, scale insects.

ORDER DERMAPTERA (Der-map′te-ra, Gr. *derma*, skin + *pteron*, wing). Commonly called **earwigs.** Metamorphosis gradual. Two pairs of wings, forewings small and leathery, hind wings larger and folded when at rest. Chewing mouth parts. Forcepslike appendages at end of abdomen. Most feed on vegetable materials, some on other insects. Found on the ground under stones or debris.

ORDER COLEOPTERA (Co′le-op′te-ra, Gr. *coleos*, sheath + *pteron*, wing). Commonly called **beetles.** Metamorphosis complete. Chewing mouth parts. Two pairs of wings, the forewings being hard and forming a sheathlike covering for the membranous hind wings and abdomen or no wings. A very numerous order feeding on all kinds of food and widely distributed. There are numerous families.

ORDER TRICHOPTERA (Tri-chop′te-ra, Gr. *thrix*, hair + *pteron*, wing). Commonly called **caddis flies.** Metamorphosis complete. Larvae aquatic, live in cases formed of sand grains or vegetable matter, have mouth parts for chewing. Adult with two pairs of membranous wings which resemble those of a moth. Mouth parts of adult vestigial.

ORDER LEPIDOPTERA (Lep′i-dop′te-ra, Gr. *lepis*, scale + *pteron*, wing). Commonly called **butterflies** or **moths.** Metamorphosis complete. Mouth parts of larva for chewing. In adult, mouth parts form a tube for sucking. Two pairs of membranous wings covered with scales or rarely wingless. Larvae usually feed on the leaves or other parts of plants. Adults suck nectar from flowers. Examples: butterflies and moths of which there are numerous families.

ORDER DIPTERA (Dip′te-ra, Gr. *dis*, two + *pteron*, wing). Commonly called **flies.** Metamorphosis complete. Larvae known as maggots. Adult with mouth parts forming a proboscis for piercing and sucking. One pair of membranous wings, the hind wings represented by small knobbed structures called halteres, or wingless. A very numerous order feeding on all kinds of food and widely distributed. Examples: crane flies, midges, mosquitoes, gallflies, black flies, horseflies, fruit flies, botflies, blowflies, houseflies.

ORDER SIPHONAPTERA (Siph′o-nap′te-ra, Gr. *siphon*, tube + *a*, without + *pteron*, wing). Commonly called **fleas.** Larval mouth parts for chewing. Metamorphosis complete. Adult without wings and with mouth parts for piercing and sucking. Body laterally compressed. Larvae feed upon waste animal matter. Adults are external parasites usually upon mammals and feed on blood. Example: human flea (*Pulex irritans*) (Fig. 24:8).

ORDER HYMENOPTERA (Hy′me-nop′te-ra, Gr. *hymen*, membrane + *pteron*, wing). Commonly called **bees, wasps, ants,** etc. Metamorphosis complete. With two pairs of membranous wings held together with hooks or without wings. Mouth parts for chewing. A numerous order living on many kinds of food and widely distributed. Examples: sawflies, ichneumon flies, gallflies, ants (Fig. 24:5), wasps, bees (Fig. 24:3).

CLASS ARACHNOIDEA (Ar′ach-noi′de-a, Gr. *arachne*, spider + *eidos*, like). These animals have no antennae and no true jaws. The first pair of appendages ends in pincers. Body is usually divided into an anterior portion consisting of a combined head and thorax, called the cephalothorax, to which the appendages are attached and a posterior part called the abdomen.

ORDER XIPHOSURA (Xiph′o-su′ra, Gr. *xiphos*, sword + *oura*, tail). Commonly called **king crabs.** There is only one living species, *Limulus*. It is a curious animal with a large helmetlike anterior portion (cephalothorax) and a small triangular abdomen. Breathing is by means of gill-hooks on the underside of the abdomen. King crab (*Limulus*) (Fig. 39:47).

ORDER SCORPIONIDA (Scor′pi-on′i-da, Gr. *skorpio*, a scorpion). Commonly called **scorpions.** The first pair of appendages end in large pincers. The abdomen is divided into a thicker portion and a long slender tail on the end of which is a sting.

ORDER ARANEIDA (Ar′a-ne′i-da, L. *aranea*, spider). Commonly called **spiders.** Spiders have four pairs of walking legs in addition to two pairs of appendages associated with the mouth (Fig. 3:22).

ORDER PHALANGIDA (Pha-lan′gi-da, L. *phalangium*, the daddy longlegs). Commonly called **harvestmen** or **daddy longlegs.** These animals are like spiders but have longer legs and there is no constriction between the cephalothorax and the abdomen.

ORDER ACARINA (Ac′a-ri′na, Gr. *akari*, a mite). Commonly called **mites** or **ticks.** These are usually small animals with an undivided rounded body. There are four pairs of walking legs. Many are parasites.

PHYLUM CHORDATA (chor-da′ta, L. *chorda*, a cord). All these animals possess at some stage in their development a chorda or notochord. This is a flexible, cellular, rodlike structure located dorsal to the alimentary canal and ventral to the central nervous system. The simpler chordates breathe by means of pharyngeal gills and have gill clefts leading from the pharynx to the exterior. All chordates show traces of this in the appearance of gill clefts at some time in their development. The central nervous system is tubular and dorsal.

Subphylum Hemichorda (Hem′i-chor′da, Gr. *hemi*, half + L. *chorda*, cord). Wormlike marine chordates. Unfamiliar animals seldom encountered by the layman but of great interest on account of the light they are believed to throw on the origin of the vertebrates. The body is divided into proboscis, collar, and trunk. The notochord is in the proboscis and collar. Breathing is by means of gills and the central nervous system is dorsal. Examples: *Dolichoglossus* (Fig. 26:2), *Balanoglossus*.

Subphylum Urochorda (U′ro-chor′da, Gr. *oura*, tail + L. *chorda*, cord). Commonly called **tunicates, ascidians,** or **sea squirts.** All of them are marine and are either free swimming or attached. Usually the free-swimming larval stage shows the chordate characters most clearly. The notochord is in the tail of the larva. The attached forms are enclosed in a leathery covering known as a tunic and composed of a substance resembling cellulose. Examples: *Ciona* (Figs. 26:3, 39:44), *Appendicularia*.

Subphylum Cephalochorda (Ceph′a-lo-chor′da, Gr. *kephale*, head + L. *chorda*, cord). Commonly called **lancelets.** Small fishlike animals lacking a distinct head. The notochord extends almost the entire length of the body, as does also the dorsal central nervous system. Breathing is by means of pharyngeal gills. Example: *Amphioxus* (Fig. 26:5).

Subphylum Vertebrata (Ver′te-bra′ta, L. *vertebratus*, backboned). In vertebrates there is an endoskeleton of cartilage or bone. Except in the most primitive forms the notochord is replaced by a vertebral column which consists of a series of ringlike segments or vertebrae. The body is divided into head and trunk and there is usually a postanal tail and there are usually (and never more than) two pairs of appendages. The anterior portion of the central nervous system is differentiated to form a brain with which are connected paired eyes and ears. The brain and sense organs are protected by a cranium or brain case. The vascular system is closed, i.e., has definite limiting walls. There is a ventral heart, a liver and hepatic portal system, and the blood contains red blood corpuscles.

CLASS CYCLOSTOMATA (Cy′clo-sto′ma-ta, Gr. *cyclos*, a circle + *stoma*, *stomata*, mouth). Commonly called **lamprey "eels,"** and **hagfish.** Long, slender, fishlike, jawless, cold-blooded, vertebrates without scales or paired fins. The skeleton is of cartilage and there is a persistent notochord. The respiratory organs consist of gills in numerous pharyngeal gill pouches communicating with the exterior. Examples: lamprey "eel" (*Petromyzon*) (Fig. 26:6), and the hagfishes (*Myxine* and *Bdellostoma*). The **Ostracoderms** (Os′stra-co-derm′, Gr. *ostracon*, shell + *derma*, skin), primitive armored fossil fishes, are believed to be closely related to the Cyclostomata.

CLASS CHONDRICHTHYES (Chon′drich-thy′es, Gr. *chondros*, cartilage + *ichthyus*, a fish). Known as **cartilaginous fishes.** Marine fishes with two pairs of lateral fins. The body is covered with placoid scales consisting of a basal plate from which projects a spine composed of dentine covered by enamel. The skeleton is cartilaginous but there is a persistent notochord. There are jaws and an almost complete cranium. Breathing is by means of platelike gills in gill slits which open separately to the outside.

ORDER ELASMOBRANCHII (E-las′mo-bran′chi-i, Gr. *elasmos*, a metal plate + L. *branchia*, gill). The **sharks** and dogfishes, and the **rays** and skates. The gill slits open separately to the outside. The upper jaw is not fused with the base of the skull. The vertebral column extends into the dorsal lobe of the caudal fin (Fig. 26:7).

ORDER HOLOCEPHALI (Hol′o-ceph′a-li, Gr. *holos*, whole + *kephale*, head). Commonly called **chimaeras.** The upper jaw is firmly attached to the cranium. Gill slits covered with a fold of skin. A very ancient group now represented only by three living genera, one of which is *Chimaera.*

CLASS OSTEICHTHYES (Os′te-ich′thy-es, Gr. *osteon*, bone + *ichthyus*, a fish). The true or **bony fishes.** Skeleton partly or entirely of bone. Paired fins. Respiration is by means of pharyngeal gills in gill slits, the latter covered on each side of the head by a bony plate known as an operculum. The body is usually covered with dermal scales, never placoid scales.

Subclass Actinopterygii (Ac′ti-nop′ter-yg′i-i, Gr. *actis*, *actinos*, ray + *pteryx*, *pterygos*, fin). **Ray-finned fishes.** The paired fins are supported by horny fin rays.

ORDER CHONDROSTEI (Chon-dros′te-i, Gr. *chondros*, cartilage + *osteon*, bone). Sturgeons and paddlefishes. Skeleton largely of cartilage but regarded as degenerated from bone. Mouth on the ventral side. Caudal fin heterocercal like that of a shark. Examples: sturgeon (*Acipenser*), paddlefish (*Polyodon*).

ORDER HOLOSTEI (Ho-los′te-i, Gr. *holos*, whole + *osteon*, bone). The skeleton is of bone and the body is covered with ganoid scales. Two living genera, *Amia* and *Lepidosteus*.

ORDER TELEOSTEI (Tel′e-os′te-i, *teleos*, complete + *osteon*, bone). Skeleton completely ossified. Scales without ganoin or enamel, thin and tending to overlap. Tail homocercal. This order contains most living fishes. Perch (*Perca*) (Fig. 39:31), Sailfish (*Istiophorus*) (Fig. 3:23), sea robin (*Prionotus*) (Fig. 39:57), shark sucker (*Echenis*) (Fig. 39:59).

Subclass Dipnoi (Dip′noi, Gr. *di*, twice + *pnoe*, breath). **Lungfishes.** Fish which breathe by means of lungs as well as gills. Skeleton is partly of cartilage. Three living genera. *Neoceratodus* occurs in Australia, *Protopterus* in Africa, and *Lepidosiren* in Paraguay.

Subclass Crossopterygii (Cros-sop′te-ryg′i-i, Gr. *crossoi*, a fringe + *pterygion*, a little fin). **Lobed-finned fishes.** An extinct group in which lungs were developed. The two living genera, *Polypterus* and *Calamiochthys* which were formerly regarded as crossopterygians, are now recognized as primitive ray-finned fishes (Actinopterygii). Recently, December 1938, a single specimen of a fish which seems to belong to this group was caught off the coast of South Africa.

CLASS AMPHIBIA (Am-phib′i-a, Gr. *amphibios* living a double life). The name refers to the animals living partly in water and partly in air. They breathe by gills in their larval or tadpole stage and through the skin and lungs when adult. In the adult stage there are two pairs of pentadactyl (i.e., five-toed) limbs without claws. The body is without scales except in certain legless tropical forms.

ORDER URODELA (U′ro-de′la, Gr. *ura*, tail + *delos*, visible). The term "Caudata" (Cau-da′ta, L. *cauda*, a tail) is also used for this order. Commonly called **salamanders** and **newts.** Tailed amphibia with the fore and hind limbs approximately equal in size. Examples: the spotted salamander (*Ambystoma*) (Fig. 3:24), the spotted newt (*Triturus*), and the mud puppy (*Necturus*).

ORDER ANURA (A-nu′ra, Gr. *a*, *an*, not + *oura*, tail). The term "Salientia" (Sa′li-en′ti-a, L. *salire*, to leap) is also used for this order. Commonly called **frogs** and **toads.** Tailless amphibia with large hind limbs adapted for jumping. Examples: leopard frog (*Rana*) (Fig. 27:1), bull frog (*Catesbiana*) (Fig. 39:24), the common toad (*Bufo*).

ORDER APODA (A-pod′a, Gr. *a*, without + *pous*, *podos*, foot). This order is also called **Gymnophiona** (Gym′no-phi′o-na, Gr. *gymnos*, naked + *ophioneos*, serpentlike). The body of these animals is wormlike without limbs or tail and there are usually small scales embedded in the skin. The order is not a large one and occurs only in the tropics. Example: *Caecilia*.

CLASS REPTILIA (Rep-til′i-a, L. *repere*, to creep). Reptiles breathe air throughout their lives. Their scales are horny and formed from the outer layer of epidermis of the skin. There are typically two pairs of appendages which are usually pentadactyl (i.e., five toed).

ORDER TESTUDINATA (Tes-tu′di-na′ta, L. *testudinatus*, a tortoise). The term "Chelonia" (Che-lo′ni-a, Gr. *chelone*, a tortoise) is also used for this order. Reptiles in which the skeleton forms a bony box which is covered by horny scales and encloses most of the body. The jaws are without teeth and covered with horn. Examples: painted turtle (*Chrysemys*) (Fig. 3:25), snapping turtle (*Chelydra*), loggerhead turtle (*Carette*) (Fig. 39:59).

ORDER RHYNCHOCEPHALIA (Rhyn′cho-ce-pha′li-a, L. *rhyncho*, snout + Gr. *kephale*, head). The order contains the single genus *Sphenodon*. Sphenodon is a lizardlike reptile about 3 feet long. Its skeleton bears many resemblances to the skeleton of the earliest reptiles and is of interest as a relic of a once numerous group which may have given rise to modern lizards and snakes. Example: *Sphenodon*.

ORDER SQUAMATA (Squa-ma′ta, L. *squamatus*, scaly). Commonly called lizards and snakes. Reptiles with horny scales and the lower jaw loosely attached to the upper jaw so that the mouth can be widely opened.

SUBORDER SAURIA (Sau′ri-a, Gr. *saura*, a lizard). The term "Lacertilia" (Lac′er-til′i-a, L. *lacertus*, a lizard) is also used for this suborder. Commonly called **lizards.** Squamata usually with well-developed limbs. Examples: American "chameleon" (*Anolis*); common or fence swift (*Sceloporus*); horned "toad" (*Phrynosoma*), skink (*Eumeces*) (Fig. 39:10).

SUBORDER OPHIDIA (O-phid′i-a, Gr. *ophis*, a snake). The term "Serpentes" (Ser-pen′tes, L. *serpens*, a serpent) is also used for this suborder. Commonly called **snakes.** Long thin-bodied squamata without limbs. Examples: the common garter snake (*Thamnophis*); common water snake (*Natrix*) (Fig. 39:30); bull snake (*Pituophis*) (Fig. 39:22).

ORDER CROCODILIA (Croc′o-dil′i-a, L. *crocodilus*, a crocodile). Commonly called **crocodiles, alligators,** and **gavials.** Usually rather large reptiles with the nostrils united to form a single opening at the end of a rather long snout. Examples: the crocodile (*Crocodylus*); the alligator (*Alligator*).

CLASS AVES (A′ves, L. *avis*, a bird). Vertebrates which are adapted for flying, the forelimbs being modified to form wings and the body covered with feathers. No living birds have teeth, their place being taken by a horny beak. When standing the weight is supported on the hind limbs.

Subclass Archaeornithes (Ar′chae-or′ni-thes, Gr. *archaios*, ancient + *ornithes*, birds). No living representatives. Contains the fossil bird *Archaeopteryx* (Fig. 40:11) described in the text. Example: *Archaeopteryx*.

Subclass Neornithes (Ne-or′ni-thes, Gr. *neos*, new + *ornis*, *ornithes*, bird). The name means "recent birds" in contrast to the older fossil birds. The subclass includes all living birds.

Division Ratitae (Ra-ti′tae, L. *ratis*, raft). The name refers to the absence of a keel on the breastbone which is related to the lack of flying muscles. Flightless terrestrial birds usually of large size. Young are precocious, being able to look after themselves from the time of hatching.

ORDER STRUTHIONIFORMES[1] (Stru′thi-on′i-for′mes, L. *struthio*, an ostrich + *forma*, appearance). Commonly called **ostriches.** Large birds which have lost the power of flight and have long legs with two toes on each foot adapted for running. They are without feathers on the head, neck, and legs. Example: the African ostrich (*Struthio*).

ORDER RHEIFORMES (Rhe′i-for′mes, L. *Rhea*, the genus of the American ostrich). Commonly called **rheas.** Large ostrichlike flightless birds with relatively few feathers on head and neck. The legs are well developed and have three toes on each foot. Example: American ostrich (*Rhea*).

ORDER CASUARIIFORMES (Cas′u-a-ri′i-for′mes, L. *cassuarius*, a cassowary). Commonly called **cassowaries** and **emus.** Ostrichlike birds with very small rudimentary wings and well-developed legs with three toes. Examples: cassowary (*Casuarius*), emu.

ORDER APTERYGIFORMES (Ap′ter-yg′i-for′mes, Gr. *a*, not + *pteryx*, wing). Apteryxlike birds. Kiwis. Small birds with hairlike feathers and rudimentary wings. Confined to New Zealand. Example: kiwi (*Apertyx*).

Division Carinatae (Car′i-na′tae, L. *carina*, a keel). The name refers to the possession of a keel on the breastbone to which the muscles of flight are attached. This division includes all living flying birds and the penguins.

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[1] The orders of birds are usually named after some representative genus, e.g., *Struthioniformes*, the ostrichlike birds.

ORDER SPHENISCIFORMES (Sphe-nis′ci-for′mes, Gr. *spheniskos*, a little wedge, the shape of the bird's wings). Commonly called **penguins.** Flightless marine birds with small scalelike feathers and wings modified to form paddles. Example: penguin (*Spheniscus*).

ORDER GAVIIFORMES (Ga′vi-i-for′mes, from *Gavia*, the loon). Commonly called **loons.** Aquatic birds with webbed toes and legs far back on body. Example: loon.

ORDER COLYMBIFORMES (Co-lym′bi-for′mes, Gr. *columbus*, a diver). Commonly called **grebes.** Aquatic birds with lobed toes. Usually smaller than loons. Example: grebe.

ORDER PROCELLARIIFORMES (Proc′el-lar′i-i-for′mes, from *Procellaria*, the stormy petrel). Commonly called **albatrosses** and **petrels.** Marine birds with powerful wings and webbed toes. Examples: stormy petrel (*Procellaria*), albatross.

ORDER PELICANIFORMES (Pel′i-can′i-for′mes, L. *pelicanus*, a pelican). Commonly called **pelicans** and **cormorants.** Aquatic swimming birds usually with fully webbed toes. Example: pelican (*Pelicanus*), cormorant.

ORDER CICONIIFORMES (Ci-co′ni-i-for′mes, L. *ciconia*, a stork). Storklike birds. Long-legged wading birds. Examples: heron (Fig. 39:29), stork, flamingo.

ORDER ANSERIFORMES (An′ser-i-for′mes, L. *anser*, a goose). Gooselike birds. Aquatic swimming birds, legs fairly short and attached near the middle so that when standing the body is horizontal. Feet webbed. Examples: goose (*Anser*), swan, duck (Fig. 39:28).

ORDER FALCONIFORMES (Fal′co-ni-for′mes, L. *falcon*, a falcon). Falconlike birds. Flesh-eating birds with curved, hooked beak and sharp claws on feet adapted for perching and seizing prey. Examples: eagle, hawk, vulture, and secretary bird.

ORDER GALLIFORMES (Gal′li-for′mes, L. *gallus*, a cock). Fowllike birds. Terrestrial or arboreal birds with feet adapted for perching and scratching. Examples: domestic fowl (*Gallus*), ruffed grouse, quail, prairie chickens (Fig. 39:20), wild turkey (Fig. 39:15).

ORDER GRUIFORMES (Gru′i-for′mes, L. *grus*, crane). Cranelike birds. Wading birds. Feet not webbed. Neck extended in flight. Examples: crane, rail.

ORDER CHARADRIIFORMES (Cha-rad′ri-i-for′mes, from *Charadrius*, a genus of plover). Ploverlike birds. Small shore birds, usually long legged and long billed. Examples: plover (*Charadrius*), gull, tern, snipe, sandpiper.

ORDER COLUMBIFORMES (Co-lum′bi-for′mes, L. *columba*, a pigeon). Pigeonlike birds. Terrestrial scratching birds with short bill and short wings. Examples: pigeon (*Columba*), mourning dove.

ORDER PSITTACIFORMES (Psit′ta-ci-for′mes, L. *Psittacus*, a parrot). Parrotlike birds. Perching birds with four toes, two in front and two behind and heavy, hooked bills. Examples: parrot (*Psittacus*), parrakeet, cockatoo.

ORDER CUCULIFORMES (Cu-cu′li-for′mes, L. *cuculus*, a cuckoo). Cuckoolike birds. Perching birds with four toes, two in front and two behind. Long compressed bill. Example: cuckoo (*Cuculus*).

ORDER STRIGIFORMES (Strig′i-for′mes, L. *strix*, a screech owl). Owllike birds. Bill hooked, eyes large in front of head surrounded by feathered discs. Claws sharp. Plumage fluffy. Example: barn owl (*Strix*), burrowing owl (Fig. 39:21).

ORDER CAPRIMULGIFORMES (Cap′ri-mul′gi-for′mes, from *Caprimulgus*, the generic name of the European goatsucker). Goatsuckerlike birds. Short-billed, widemouthed birds with long pointed wings and fluffy plumage. Examples: nighthawk, whippoorwill.

ORDER MICROPODIFORMES (Mi′cro-po′di-for′mes, Gr. *mikros*, small + *pous*, *podos*, foot). Swiftlike birds with small feet. Either very small birds with long slender bill (hummingbirds) or somewhat larger birds with very short bill and wide mouth (swifts).

ORDER CORACIIFORMES (Cor′a-ci′i-for′mes, Gr. *corax*, a crow). Kingfisherlike birds. Bill straight, pointed, and long. Legs small. Examples: kingfisher, hornbill; but not the crows, for which see Passeriformes.

ORDER PICIFORMES (Pic′i-for′mes, L. *picus*, a woodpecker). Woodpeckerlike birds. Climbing birds with heavy pointed bills and stiff tail feathers used to prop the body against trees. Examples: woodpecker (Fig. 39:14), toucan.

ORDER PASSERIFORMES (Pas′ser-i-for′mes, L. *passer*, a sparrow). Sparrowlike birds. Small or medium-sized perching birds or song birds. The largest order of birds containing more than half of the known species. Examples: flycatchers, larks, swallows, crows, jays, chickadees (Fig. 3:26) or titmice, nuthatches, wrens, thrushes, robins, waxwings, starlings, vireos, wood warblers, weaver finches, blackbirds, sparrows.

CLASS MAMMALIA (Mam-ma′li-a, L. *mamma*, breast). The name refers to the method of nourishing the young with milk from mammae or breast glands. Mammals are also distinguished by the possession of hair.

Subclass Prototheria (Pro′to-the′ri-a, Gr. *protos*, first + *therion*, beast). The term **Monotremata** (Mon′o-tre′ma-ta, L. *mono*, one + *trema*, hole) is also used for this subclass. Primitive egg-laying mammals with a cloaca. The subclass is confined to Australia, Tasmania, and New Guinea. Examples: duckbill (Fig. 3:27), spiny "anteater."

Subclass Metatheria (Met′a-the′ri-a, Gr. *meta*, between + *therion*, beast). The term **Marsupialia** (Mar-su′pi-a′li-a, L. *marsupium*, pouch) is also applied to this subclass. Often called **marsupials** or **pouched mammals.** Mammals in which the young are born in a very immature state and are usually carried in a pouch. With the exception of the opossums they are confined to Australia and neighboring islands. Examples: opossum, kangaroo (Fig. 3:28), phalanger, wombat, bandicoot, koala.

Subclass Eutheria (Eu-the′ri-a, Gr. *eu*, well + *therion*, beast). The term **Placentalia** (Plac′en-ta′li-a, Gr. *placenta*, a flat cake) is also applied to this subclass. Commonly called **placental mammals.** Mammals in which the mother retains the young in her body for a considerable time, nourishment being provided through a special organ known as the placenta. Since this class includes our best-known mammals the classification will be carried further.

ORDER INSECTIVORA (In′sec-tiv′or-a, L. *insectum*, an insect + *vorare*, to devour). Small insect-eating, clawed mammals with primitive teeth and nervous system. Example: mole (Fig. 26:12), shrew.

ORDER CHIROPTERA (Chi-rop′ter-a, Gr. *cheir*, hand + *pteron*, wing). Flying mammals with the forelimbs modified for flight. Example: bat (Fig. 26:13).

ORDER CARNIVORA (Car-niv′o-ra, L. *caro*, *carnis*, flesh + *vorare*, to devour). Flesh-eating mammals with claws and large projecting canine teeth. Examples: wolf, racoon, badger (Fig. 39:19), skunk, cat, lion (Fig. 3:29).

ORDER PINNIPEDIA (Pin′ni-pe′di-a, L. *pinna*, a fin + *pes*, *pedis*, foot). This order is sometimes included in the Carnivora. The seals and their relatives. These animals differ from carnivores chiefly in their limbs which are finlike. The teeth specialized, the external ear much reduced or absent, tail very short or absent. Examples: seal, sea lion, walrus.

ORDER PRIMATES (Pri-ma′tes, L. *prima*, *primatis*, one of the first). Mammals with five digits on the fore and hind limbs and nails on the digits. Fore and hind feet often adapted for grasping. Orbit surrounded by bone. Examples: monkey, ape (Fig. 26:15), man.

ORDER EDENTATA (E′den-ta′ta, L. *e*, without + *dens*, *dentis*, tooth). Clawed mammals with teeth without enamel and no teeth in the front of the mouth. Once thought to be primitive forms, now considered specialized with degenerate teeth. Examples: American anteater, sloth (Fig. 26:16), armadillo.

ORDER PHOLIDOTA (Phol′i-do′ta, Gr. *pholis*, scale + *osis*, state). Scaly anteaters. Body covered with overlapping epidermal scales. Example: Pangolin or scaly anteater.

ORDER RODENTIA (Ro-den′ti-a, L. *rodare*, to gnaw). Gnawing mammals with two prominent incisors in each jaw which are chisel-shaped and without enamel on the posterior surface, no canine teeth and clawed feet. Small to moderate sized. The most numerous order of mammals. Examples: mice (Fig. 39:11), rats, squirrels (Fig. 39:12), prairie dog (Fig. 39:18), chipmunks (Fig. 26:17), guinea pigs, porcupines, muskrats (Fig. 39:27), beavers.

ORDER LAGOMORPHA (Lag′o-mor′pha, Gr. *lagor*, a hare + *morphe*, form). This order is sometimes included in the Rodentia. These animals resemble rodents but differ from them in having four instead of two upper incisors. Examples: rabbit and hare.

ORDER HYRACOIDEA (Hy′ra-coi′de-a, Gr. *hyrax*, the name of an animal).

Small rodentlike mammals. Forelimbs with four digits, hind limbs with three. Only one living genus. Example: coney.

ORDER ARTIODACTYLA (Ar′ti-o-dac′ty-la, Gr. *artios*, even + *dactylos*, toe). Even-toed, hoofed mammals (ungulates). The first toe is suppressed and the weight on each foot is carried by four, or more often, two toes. Examples: pig, hippopotamus, deer (Fig. 39:13), camel, giraffe, cow, buffalo (Fig. 39:23).

ORDER PERISSODACTYLA (Pe-ris′so-dac′ty-la, Gr. *perissos*, odd + *dactylos*, toe). Odd-toed hoofed mammals (ungulates). The third toe is the largest and carries more of the weight on the foot than the others. Examples: horse, tapir, rhinoceros.

ORDER PROBOSCIDEA (Pro′bos-cid′e-a, Gr. *pro*, before, + *boscein*, to feed). Elephants. Two upper incisors form tusks, nose forms a long "trunk" or proboscis. Example: elephant.

ORDER SIRENIA (Si-re′ni-a, Gr. *seiren*, a sea nymph). Manatees or sea cows. Large herbivorous aquatic mammals with broad crushing teeth. Forelimbs are finlike, hind limbs absent, tail rounded. Example: sea cow.

ORDER CETACEA (Ce-ta′ce-a, L. *cetus*, a whale). Fishlike mammals with finlike forelimbs and no hind limbs. The tail takes the form of a horizontal fluke. There is no external ear. The eyes are minute. The skin is almost hairless. In some classifications this order is represented as two orders: Order Odontoceti (O-don′to-ce′ti, Gr. *odous*, *odontos*, tooth + *cetos*, whale), the toothed whales; and Order Mystacoceti (Mys′ta-co-ce′ti, Gr. *mystax*, mustache + *cetos*, whale), the whalebone whales. Examples: whales, dolphins (Fig. 26:18).

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